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SYSTEMATICS AND ECOGEOGRAPHIC VARIATION OF THE APACHE POCKET MOUSE (RODENTIA: HETEROMYIDAE)

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ABSTRACT

Geographic variation in *Perognathus apache* Merriam and the systematic relationships of *P. fasciatus* Wied-Neuwied and *P. flavescens* Merriam with *P. apache* were investigated. Most geographic variation was attributable to a relatively few climatic and geographic factors. A strong north-south size cline, with small mice in the warmer, southern latitudes and large mice in the colder, northern latitudes was observed. The posterior cranial region became progressively more constricted with increasing size, and the length of the tail increased at a rate faster than the length of the head and body. Body size was inversely correlated with mean annual temperature, size of the auditory bullae was inversely correlated with mean annual precipitation, and the size of the rostrum increased with increasing aridity. A color index, relative darkness, was highly correlated with mean annual precipitation. These patterns of variation were as predicted by principles of ecogeographic variation, except for length of the tail, which increased with increasing latitude and decreasing mean annual temperature. It is hypothesized that the tail is important for maintaining balance while foraging, and that as size increases, relative tail length increases to maintain proper balance.

Populations of *P. apache* and *P. flavescens* were found to have identical karyotypes and to be closely similar in structure. *Perognathus apache* is considered to be conspecific with *P. flavescens*. Four intermountain races of the plains pocket mouse are recognized—*P. flavescens apache, P. f. caryi* Goldman, *P. f. melanotis* Osgood, and *P. f. relictus* Goldman. The race *P. f. cleomophila* Goldman is a junior synonym of *P. f. apache*, and the race *P. f. gypsi* Dice is a junior synonym of *P. f. melanotis*.

INTRODUCTION

The Apache pocket mouse is a small, sand-inhabiting, desert-adapted rodent belonging to the genus *Perognathus* of the family Heteromyidae. It occurs on the intermountain plateaus from Chihuahua northward into the Uintah Basin of Utah and Colorado, ranging from the upper Pecos and Rio Grande valleys in the east to near San Francisco Peaks and the Grand Canyon in the west (Fig. 1). *Perognathus apache* was described by C. H. Merriam (1889) in the first revision of *Perognathus*. The holotype was collected near Keam's Canyon, Navajo Co., Arizona. Merriam considered *P. apache* to be most similar to *P. inornatus* Merriam, 1889, from the Central Valley of California. Osgood (1900), in the only other revision of *Perognathus*, named an additional race of the Apache pocket mouse, *P. a. melanotis* from Casas Grandes, Chihuahua. He thought that *P. apache* was closely related only to *P. callistus* Osgood, 1900 (=*P. fasciatus callistus*). He remarked on the resemblance between *P. apache* and *P. inornatus* (*P. inornatus* Merriam, 1889 = *P. longimembris* of Osgood, 1900), but considered the great distance between their ranges to belie a close relationship. Goldman (1918) subsequently described two additional subspecies of Apache pocket mice, *P. a. cleomophila* from the black lava sands near Flagstaff, Arizona, and *P. a. caryi* from the Grand River Valley of Garfield Co., Colorado. Next, Dice (1929) described a new species of pocket mouse, *P. gypsi*, from the White Sands of the Tularosa Basin, New Mexico. Benson (1933*a*) later arranged this nearly white form as a subspecies of *P. apache*. Finally, Goldman (1938) named a subspecies, *P. a. relictus*, which occurs on the Great Sand Dunes of the San Luis Valley of Colorado.

Prior to the initiation of this study, *P. apache* was allied with four other species in the *fasciatus* group (Osgood, 1900), including *P. fasciatus* Wied-Neuwied, 1838, *P. flavescens* Merriam, 1889, *P. flavus* Baird, 1855, and *P. merriami* Allen, 1892. *Perognathus apache* was generally regarded as being most closely related to *P. fasciatus* of the northern Great Plains (Fig. 1). Harris (1965) proposed that *P. apache* was conspecific with *P. fasciatus*. *Perognathus fasciatus* was also thought to be closely related to *P. flavescens* of the central and southern Great Plains (Fig. 1). In fact, Merriam (1889) originally described *flavescens* as a subspecies of *P. fasciatus*. Osgood (1900) elevated *P. flavescens* to specific status, noting that both forms occurred at the Rosebud Indian Agency, South Dakota, without apparent hybridization. The two species are now known to be sympatric over a broad area (Fig. 1). Osgood (1900) believed that *P. flavescens* was possibly conspecific with *P. merriami*, and suggested that intergradation might occur through *P. copei* Rhoads, 1893 (=*P. flavescens copei*), which he regarded as being synonymous with *P. flavescens*. Blair (1954) also thought that *P. flavescens* and *P. merriami* were closely related, and proposed that the two forms diverged from a common ancestor during Wisconsin or post-Wisconsin changes in the distribution of grasslands in the southern Great Plains. Earlier, Blair and Miller (1949) noted a close resemblance between *P. flavus* and *P. merriami*, as had other workers (Osgood, 1900; Bailey, 1932). Patton (1967) demonstrated a close similarity be-

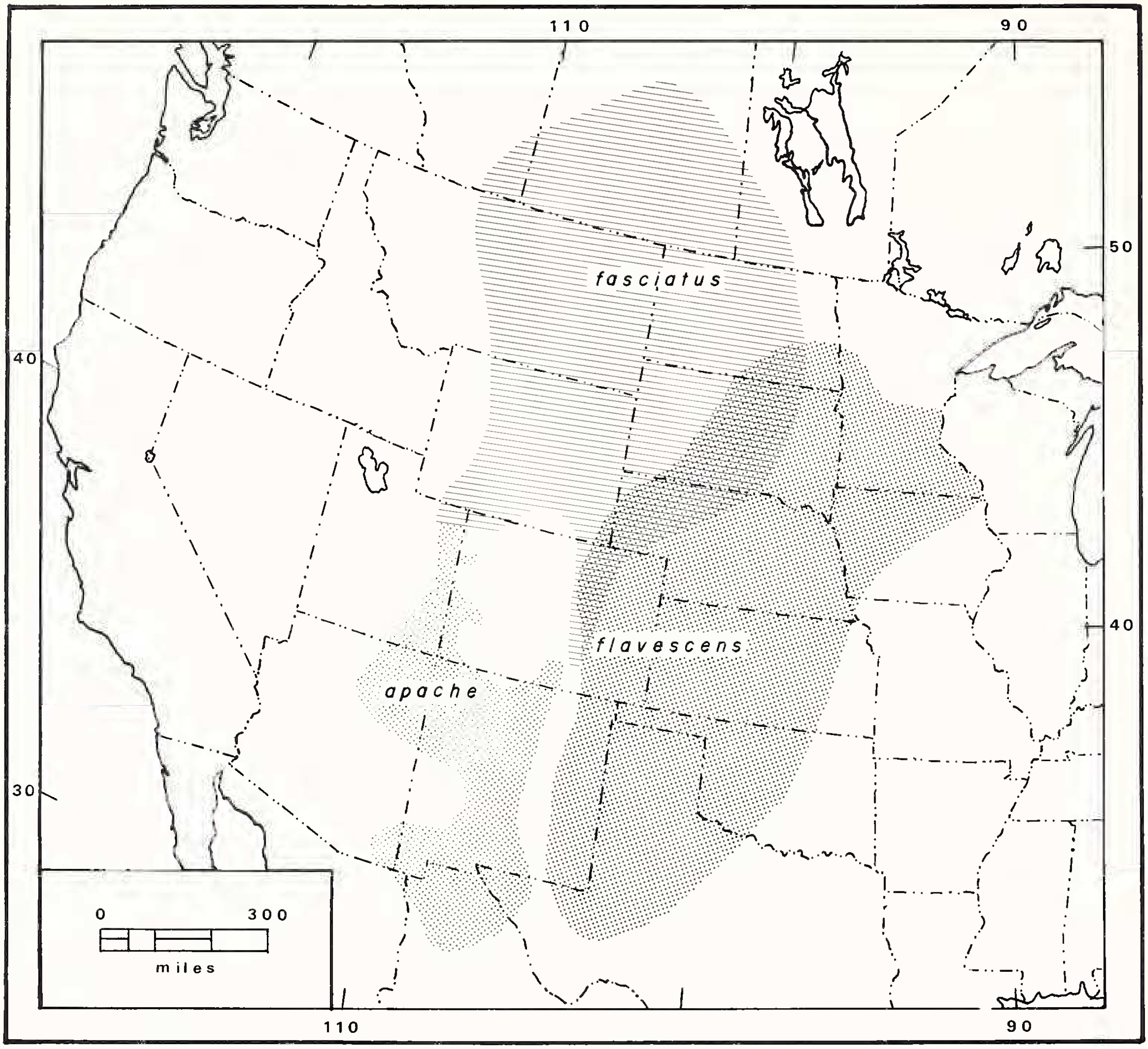

Fig. 1.—Distribution of *Perognathus fasciatus* species group.

tween the karyotypes of *P. flavus* and *P. merriami*, and noted that these taxa differ in chromosome structure from *P. amplus* Osgood, 1900, *P. longimembris* (Couse, 1875), and *P. parvus* (Peale, 1848). Wilson (1973) later reported that *P. merriami* was conspecific with *P. flavus*.

I undertook studies of *Perognathus* in order to clarify the specific status of *P. apache* and to define the interspecific relationships of the species of the *fasciatus* group. In another paper (Williams, 1978), using chromosome structure, I demonstrated that *P. flavus merriami* is only distantly related to *P. flavescens*, and redefined Osgood's (1900) species groups, limiting membership in the *fasciatus* group to *P. fasciatus*, *P. flavescens*, and *P. apache*. These latter three species have nearly identical karyotypes, and are widely divergent in chromosome structure to other members of the subgenus *Perognathus*. In that paper, I proposed a model for the evolution of the species groups of the subgenus *Perognathus*. When I initiated these studies, Dr. Robert Packard had undertaken a review of the geographic variation in the plains pocket mouse, *P. flavescens*. For this reason, I have made no attempt to review the systematics of that species. A systematic review of *P. fasciatus* is under study, and will be reported elsewhere. This paper presents an analysis of the geographic variation of the Apache pocket mouse, and explores its relationships to *P. flavescens* and *P. fasciatus*.

METHODS AND ACKNOWLEDGMENTS

I conducted field studies during the warmer months (generally May through September) of 1967 through 1970. I visited most of the known collecting localities of *P. apache* to examine adjacent localities for habitat continuity, and to collect specimens for morphologic and karyotypic studies. Generally, I set between 200 and 300 traps per night, relocated the traps each night, and usually checked and removed animals from the traps one or two times after dark. Except for the summer months of 1967, when I set both Museum Special snap traps and Sherman live traps, I set only Sherman traps (primarily the small, 5 by 6.4 by 16.5 cm size). Trapping results during 1967 suggested that moonlight severely curtailed surface activity of Apache pocket mice; thus, in subsequent years most field work was done when there was little or no moonlight. Nearly all trapping was done in areas that had either yielded specimens of *P. apache* previously, or where the habitat seemed favorable for this species. Most collecting activities were conducted in peripheral areas of the range of *P. apache*. Most traps were set in favorable habitats (primarily loose, sandy soils with sparse vegetation), but some traps (generally 45 to 100) were nearly always set in adjacent areas with harder-packed soils and in areas with denser vegetation. In addition to trapping, I also searched for pocket mice by lantern light for 1 to 4 h after dark on most evenings.

Preparations of metaphase chromosomes were secured from 53 specimens, representing all of the subspecies of *P. apache*, three subspecies of *P. fasciatus*, and *P. flavescens copei* (see lists of specimens examined). The methods and a comparative karyological treatment of the species of the subgenus *Perognathus* are given elsewhere (Williams, 1978). Only data pertinent to the present study will be discussed here.

Thirty morphometric characters were utilized (Table 1). Dial calipers were used to measure the cranial traits depicted in Fig. 2. Dental measurements were taken with an ocular micrometer in a dissecting microscope. All dental measurements were taken from occlusal view, and represent greatest length and greatest width of the teeth. Standard external measurements were as recorded on specimen tags. For specimens I prepared, length of ear and length of hind foot were taken with vernier calipers. Because many early collectors did not measure the ear, most of the multivariate analyses did not include this character.

Color was analyzed subjectively. Two color parameters were scored for each skin with adult pelage. Two individuals were selected as color standards and were assigned a numerical value for each parameter. One, darkness, is the degree of darkness produced by the relative number of black-tipped hairs on the dorsal and lateral surfaces. The other, richness, is the quality of the color produced by yellowish pigments in the terminal or subterminal bands of the dorsal and lateral hairs. This parameter ranges from white (no pigment) through a rich yellowish-orange, closest to Ochraceous-Orange or Ochraceous-Tawny (all capitalized colors are from Ridgway, 1912). Specimen MSB 17848 from 5 mi N, 6 mi E Newcomb, San Juan County, New Mexico, was the lighter, less rich color standard, and was assigned values of 2 for both darkness and richness. Specimen MSB 12598 from 4 mi N, 2 mi W Estrella, McKinley County, New Mexico, was assigned values of 4 for both darkness and richness. All other specimens of *P. apache* and *P. flavescens* were compared with the two standards. If an individual had less of a blackish overwash than the 2 standard, it was assigned a value of 1 for darkness; if it appeared to have the same amount as the 2 standard, it received a score of 2. Specimens intermediate to the standards were assigned values of 3, and those darker than 4 were given scores of 5. Specimens without black-tipped hairs received a score of 0 for darkness. Richness was quantified independently and in the same manner. The dominant wavelength of the yellowish color did not appear to vary in the samples of *P. apache* and *P. flavescens*, but the concentration of the pigment varied from none (white, with a value of 0) to high (dark Ochraceous-Tawny, with a value of 5). Because both darkness and richness contribute to an appearance that varies from light (much reflected light) to dark (little reflected light), combining these indices

Table 1.—*Morphometric traits utilized on this study. Measurements are in mm.*

No.	Trait	Abbreviation	Decimal recorded
1.	Total length	TOTL	1.00
2.	Length of tail	TL	1.00
3.	Length of head and body	HBL	1.00
4.	Length of hind foot	HFL	1.00
5.	Length of ear	EL	0.10
6.	Tail/head and body ratio	TL/HBL	—
7.	Greatest length of skull	GLS	0.05
8.	Occipitonasal length	ONL	0.05
9.	Interorbital breadth	IOB	0.05
10.	Length of maxillary toothrow (alveolar)	MXTL	0.05
11.	Width across maxillary toothrow	WMXT	0.05
12.	Bullar length	BL	0.05
13.	Width across bullae	BW	0.05
14.	Length of interparietal	IPL	0.05
15.	Width of interparietals	IPW	0.05
16.	Length of nasal	NL	0.05
17.	Width of nasals	NW	0.05
18.	Width of rostrum	RW	0.05
19.	Least interbullar distance	LID	0.05
20.	Length of mandibular toothrow	MNTL	0.05
21.	Length of P_4	P_4L	0.03
22.	Width of P_4	P_4W	0.03
23.	Length of M_3	M_3L	0.03
24.	Width of M_3	M_3W	0.03
25.	Length of articular process	LAP	0.05
26.	Width of P^4	P^4W	0.03
27.	Width of M^1	M^1W	0.03
28.	Width of M^3	M^3W	0.03
29.	Length of M_1	M_1L	0.03
30.	Width of M_1	M_1W	0.03

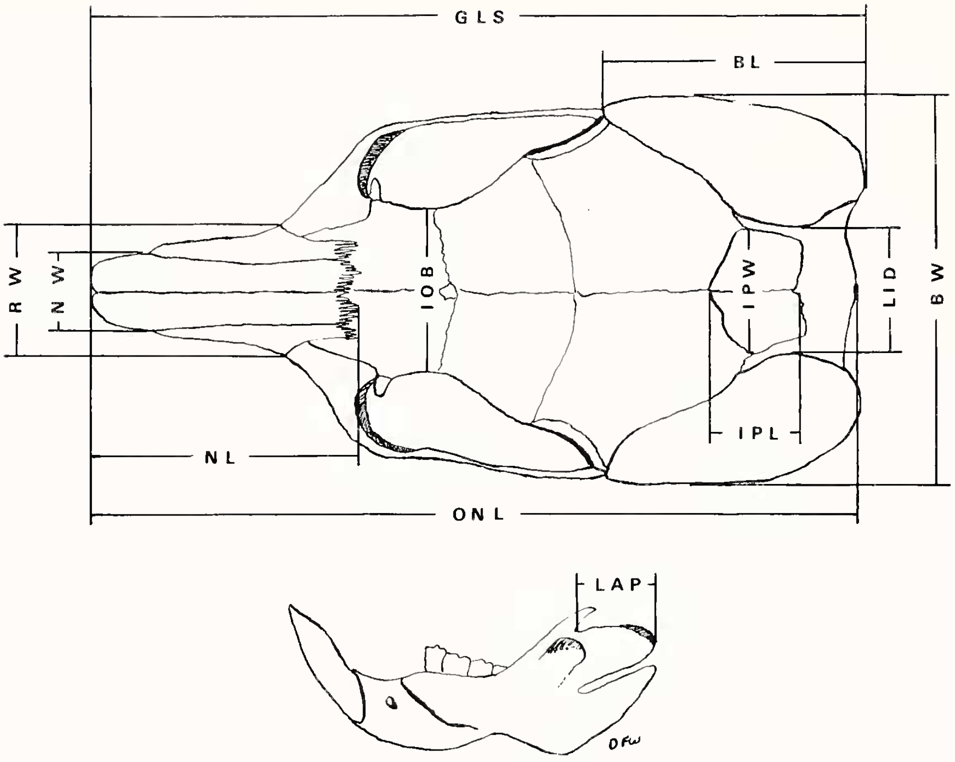

Fig. 2.—Cranial measurements used in this study. Measurements are identified in Table 1. Alveolar length of maxillary toothrow and length of mandibular toothrow are now shown.

expresses the relative darkness of the specimens. Animals with large numbers of black-tipped hairs (for example, a score of 5 for darkness), and with little yellowish pigment (a score of 1 for richness) would score the same relative darkness (6) as a mouse intermediate for darkness (3) and richness (3). Samples of *P. fasciatus* were not compared with the color standards because that species has a qualitative difference in the yellowish pigment. Because these color data were ordinal, and because color was much more variable than were the morphometric traits, these data were not used in the multivariate analyses.

Climatic and geographic data were obtained from the 1960 Ten Year State Summaries of Climatic Data, U.S. Weather Bureau. Where elevation or latitude of the collecting localities differed from the nearest weather stations, these data were obtained from the 1970 editions of Sectional Aeronautical Charts. The climatic and geographic variables used were mean duration of the frost-free period (growing season), mean annual precipitation, mean annual temperature, mean July minimum temperature, elevation, latitude, elevation adjusted for latitude (latitude × 350 + elevation), and a climatic severity index, calculated by dividing the elevation adjusted for latitude by the growing season.

Specimens were sorted into five age classes on the basis of dental characters. Individuals with deciduous upper premolars, and with no evidence of the permanent premolars, were assigned to Age Class 1 (Fig. 3). Individuals with deciduous premolars, and with permanent premolars clearly visible beneath the eroded roots of the deciduous teeth comprised Age Class 2. The permanent P^4 was not at occlusal level and its cusps were unworn for individuals of Age Class 3. Individuals of Age Class 4 had the P^4 at occlusal level and there was moderate wear on the cusps of P^4, M^1, and M^2. The P^4 cusps of Age Class 5 individuals were worn to where at least the metaloph cusps were obliterated.

For statistical analyses, Age Classes 1 and 2 were grouped as juveniles. Individuals of Age Class 3 (subadults) were treated separately, and individuals of Age Classes 4 and 5 (adults) were grouped together. Statistical comparisons were made between juveniles, subadults, and adults from the four localities with the largest samples (Uintah Basin, San Juan Basin, Painted Desert, and Rio Grande Valley). Male and female adults of these samples were also compared.

Standard univariate statistics included mean, variance, standard deviation, standard error of the mean, range, and coefficient of variation, and were computed by a program in the Biomedical Computer Programs series (BMD, Dixon, 1976), or by a program developed by me (DFW). The sums of squares simultaneous testing procedure (SS-STP, Gabriel, 1964) was performed using the UNIVAR program. This program employs a single-classification analysis of variance to test for differences between or among means ($P \leq 0.05$), and is used to determine maximally nonsignificant subsets. Student's *t*-tests were two-tailed, and were performed using both pooled and separate variance estimates (BMD), or separate variance estimates only (DFW).

Factor analysis (BMD08M) utilized matrices of correlation for factor extraction. The diagonal elements in the matrices of correlation were not altered, and intial communality estimates were the maximum absolute row values. Analyses included both orthogonally rotated and unrotated factor matrices (Dixon, 1976). Because the unrotated factor matrix met the main requirements of simple structure (Wallace and Bader, 1967) and because I found that the rotated matrix could not be as easily interpreted in a biological context, only the unrotated matrix is presented.

Stepwise discriminant function analysis and canonical analysis (BMD07M) are techniques that define and separate groups and identify unknown specimens. The program performs a multiple discriminant analysis in a stepwise manner, selecting the variable entered by finding the variable with the greatest F value. The F value for inclusion was set at 0.01, and the F value for deletion was set at 0.005. Canonical coefficients are derived by multiplying the coefficient of each discriminant function by the mean of each corresponding variable. The program also classifies individuals, placing them with the group that they are nearest to on the discriminant functions.

The MINT programs are a package of numerical taxonomic routines (Rohlf, 1971). Data were standardized for all of the analyses by the MINT programs. Phenograms were constructed by the unweighted pair-group method using arithmetic averages (UPGMA, Sneath and Sokal, 1973). The coefficients of similarity were derived from a Q-mode correlation analysis. Coefficients of taxonomic distance are average Euclidean distances. The principal components were extracted from a matrix of correlation. A seven-centroid solution to the distance matrix was computed using the K-Centroid program (MINT). This program partitions a set of OTU's into a specific number of groups, such that the sum of the taxonomic distances of each OTU to its closest centroid is a minimum. The potential centroids are limited to the OTU's present in the data set (Rohlf, 1971).

Preliminary groupings of samples were made only for immediately adjacent localities (less than 15 to 20 km distance) that were ecologically similar and continuous. Then, if no significant differences were found between localities that were both similar and continuous ecologically, they were combined. This process resulted in four samples of *P. fasciatus*, two samples of *P. flavescens*, and 15 samples of *P. apache* that were utilized in the univariate and multivariate analyses. A few specimens from scattered localities, such as along the lower San Juan River in Utah and near Navajo Mountain in Arizona, were not included in the morphometric analyses. The specimens examined are listed in the systematic accounts. The geographic localities for all samples are shown in Fig. 4. The number and name codes for these samples are as follows: 1—*P. f. fasciatus;* 2—*P. f. olivaceogriseus;* 3—*P. f. litus;* 4—*P. f. callistus;* 5—*P. apache*, Uintah Basin; 6—*P. apache*, Moab; 7—*P. apache*, Painted Desert; 8—*P. apache*, Flagstaff; 9—*P. apache*, Gallup; 10—*P. apache*, San Juan Basin; 11—*P. apache*, Canyon Largo; 12—*P. apache*, Estrella; 13—*P. apache*, San Luis Valley; 14—*P. apache*, Santa Fe; 15—*P. apache*, Rio Grande Valley; 16—*P. apache*, San Augustine Plains; 17—*P. apache*, Gran Quivira; 18—*P. apache*, White Sands; 19—*P. apache*, Deming Plains; 20—*P. flavescens copei;* 21—*P. f. flavescens*.

The following institutions provided specimens for this study. The abbreviations preceding the institutions are used in the accounts to identify the disposition of specimens. Addresses and curators in charge of the collections can be obtained from Choate and Genoways (1975). Specimens of institutions marked with an asterisk were not included in the statistical analyses. All were, however, measured and checked for conformity with the conclusions based on the statistical results.

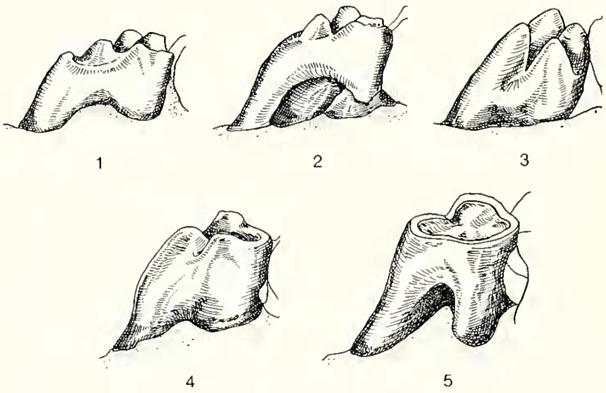

Fig. 3.—Labial view of right upper fourth premolars, representing age classes 1 through 5. 1 and 2 = deciduous premolars; 3, 4, and 5 = permanent premolars.

AMNH—American Museum of Natural History, New York.
BS—Biological Survey Collections, National Fish and Wildlife Laboratory, Washington, D.C.
CAS—California Academy of Sciences.*
CM—Carnegie Museum of Natural History, Pennsylvania.
DCBML—U.S. Bureau of Sport Fisheries and Wildlife, Ft. Collins, Colorado.
ENMU—Eastern New Mexico University.
FMNH—Field Museum of Natural History, Illinois.*
KSU—Kansas State University.*
KU—University of Kansas, Museum of Natural History.
LACM—Los Angeles County Museum, California.
MALB—University of Texas, El Paso, Museum of Arid Land Biology.
MMNH—University of Minnesota, James Ford Bell Museum of Natural History.*
MNA—Museum of Northern Arizona.*
MSB—Museum of Southwestern Biology, University of New Mexico.
MVZ—University of California, Berkeley, Museum of Vertebrate Zoology.
MWU—Midwestern University, Texas.*
NMSU—New Mexico State University.
SIUC—Southern Illinois University.*
TCWC—Texas Cooperative Wildlife Collections, Texas A&M University.*
UA—University of Arizona.
UCM—University of Colorado Museum.
UIMNH—University of Illinois, Museum of Natural History.*
UMMZ—University of Michigan, Museum of Zoology.*
UNSM—University of Nebraska, State Museum.*
UU—University of Utah.
VMKSC—Kearney State College, Vertebrate Museum, Nebraska.*

Acknowledgments

This study was initiated at the University of New Mexico in conjunction with a Master's thesis entitled "The geographic variation of the Apache pocket mouse in New Mexico," and

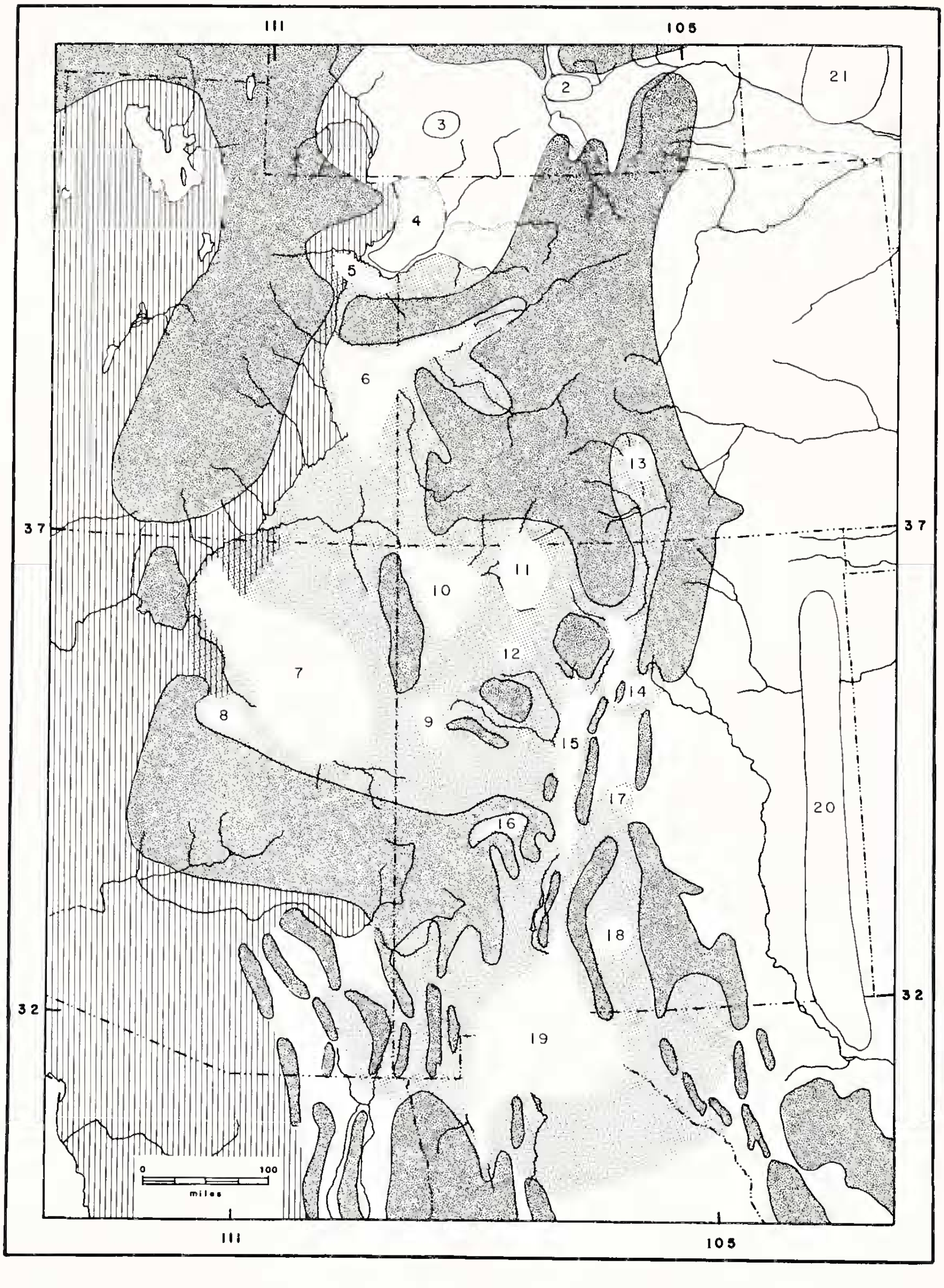

Fig. 4.—Map showing distribution of *Perognathus apache* samples used in the statistical analyses. Numbered, white areas within the lightly stippled area represent the positions of the *P. apache* samples (as defined in the text and in Table 7). Numbered areas aurrounded by unshaded areas represent samples of *P. fasciatus* (2–4) and *P. flavescens* (20, 21). Line-shaded areas represent the combined ranges of the *P. longimembris* and *P. parvus* species groups. The lightly stippled area represents the range of *P. apache*. Darkly shaded areas represent mountainous regions that may serve as barriers to the dispersal of *P. fasciatus* group pocket mice.

grew into a Ph.D. dissertation, "The systematics and evolution of the *Perognathus fasciatus* group of pocket mice." After the completion of that phase, the project lay dormant for nearly seven years. A sabbatical leave from California State College, Stanislaus and a research appointment at the Carnegie Museum of Natural History provided the time and resources to bring this project to completion. This report is based upon a portion of the data gathered for my dissertation. Most of the analyses are new and I have examined about 200 additional specimens that were previously unavailable.

Table 2.—*Summary of trapping results. The total number of traps set varies for the different species, as only traps set within their ranges are counted.*

		Captures				Substrate	
Target species and associates	Traps set	By traps	%	By hand	Total	Sand	Other
Perognathus apache	12,296	128	1.0	20	148	118	30
Perognathus flavus	10,261	198	1.9	40	238	28	210
Perognathus parvus	565	28	5.0	0	28	0	28
Perognathus penicillatus	3,629	31	0.9	0	31	25	6
Perognathus amplus	280	16	5.7	0	16	0	16
Perognathus intermedius	870	1	0.1	0	1	0	1
Dipodomys ordii	12,296	833	6.7	13	846	602	244
Dipodomys merriami	5,240	375	7.2	0	375	297	78
Peromyscus spp.	12,296	287	2.3	0	287	183	104
Onychomys spp.	12,296	264	2.1	3	267	213	51
Reithrodontomys spp.	12,296	24	0.2	0	24	20	4
Other nocturnal species	12,296	34	0.3	5	39	26	13
Diurnal species	12,296	10	0.1	0	10	8	2
Perognathus fasciatus	2,095	48	1.7	0	48	32	16
Perognathus parvus	150	1	0.6	0	1	0	1
Dipodomys ordii	2,095	133	6.3	0	133	84	49
Peromyscus maniculatus	2,095	340	16.2	0	340	276	64
Onychomys leucogaster	2,095	15	0.7	0	15	13	2
Reithrodontomys spp.	2,095	4	0.2	0	4	3	1
Other nocturnal species	2,095	7	0.3	0	7	0	7
Diurnal species	2,095	15	0.7	0	15	8	7
Perognathus flavescens	1,229	11	0.9	0	11	11	0
Perognathus flavus	1,229	1	0.1	0	1	0	1
Dipodomys ordii	1,229	200	16.3	0	200	200	0
Dipodomys merriami	869	5	0.6	0	5	0	5
Peromyscus maniculatus	1,229	21	1.7	0	21	21	0
Onychomys leucogaster	1,229	28	2.3	0	28	28	0

The University of New Mexico provided financial assistance in the form of assistantships and an NDEA Title IV fellowship. I am grateful for that assistance, and for the equipment and facilities furnished by the University. Dr. Arthur H. Harris laid the groundwork for this study with his collection of Apache pocket mice and his investigation into their relationship with the olive-backed pocket mouse. Dr. James S. Findley suggested the original project, and gave advice and encouragement along the way. Several of my fellow students aided my studies. Kenneth Andersen, Hal Black, Gwen Britt, Michael Bogan, Jay Drueck-er, Kenneth Geluso, and Don Wilson were particularly helpful. California State College, Stanislaus paid a portion of my travel expenses incurred in examining holotypes. The Carnegie Museum of Natural History furnished computer time at Carnegie-Mellon University. Teresa Bona typed the manuscript, and Nancy Perkins drew Figs. 3 and 6. Suzanne Braun and Hugh H. Genoways have been especially helpful in editing drafts of this report. James L. Patton and Robert E. Martin critically reviewed a draft of this paper, and offered several suggestions for improving it. A special note of appreciation is extended to these persons and to the many curators and curatorial assistants who made specimens available for study.

RESULTS AND DISCUSSION

Distribution and Habitat

A summary of the relevant capture data is presented in Table 2. A total of 522 individuals of *Perognathus* was captured, representing 16.5% of the small mammals taken. A majority of traps were set in sandy areas, and no attempt was made to sample all habitats or to sample different habitats equally. The small traps undoubtedly reduced the catch of larger species, including *Dipodomys*. Even so, kangaroo rats were captured from six to 16 times more frequently than were *fasciatus* group pocket mice. The silky pocket mouse, *P. flavus*, was captured twice as often as *P. apache*, despite a trapping regimen that was designed to maximize the catch of *P. apache*.

Apache pocket mice are usually limited to loose, sandy soils and dunes with a sparse vegetational cover. I often captured them on sand dunes, several hundred feet from the nearest vegetation. One exception was in the Unitah Basin of Utah, where I found *P. apache* to be common and widespread on a variety of substrates. In the Navajo Reservoir area of northwestern New Mexico, Harris (1963) captured two specimens on fine-textured soils. Some specimens from adjacent areas in Colorado may have come from similar habitats. Twice, in northwestern New Mexico and southeastern Utah, I took single specimens on hard-packed, fine-textured soils along arroyos. In both cases, I captured several specimens in adjacent, sandy areas.

The geographic distribution of *P. apache* is shown in Fig. 4. Apache pocket mice are most numerous in steppe-grassland associations between 5,000 and 7,500 ft in elevation. Common plant associates are sagebrush (*Artemisia*), saltbush (*Atriplex*), mormon tea (*Ephedra*), snakeweed (*Gutierrezia*), juniper (*Juniperus*), rice grass (*Oryzopsis*), tumbleweed (*Salsola*), yucca (*Yucca*), and rabbit bush (*Chrysothamnos*). *P. apache* ranges from Lower Sonoran mesquite associations through lower Transition pinyon-juniper associations. It is recorded as occurring in the yellow-pine zone in the Gallina Mountains of New Mexico (Bailey, 1932). That locality is actually a stabilized dune system at the northeastern edge of the San Augustine Plains, where scattered yellow pines (*Pinus ponderosa*) extend onto an old dune system that abuts against the mountains. I, and others, have also taken *P. apache* among scattered yellow pines in the vicinity of Winona, east of Flagstaff, Arizona. There, mice were captured on lava sands among rabbit bush, sagebrush, and juniper, with scattered yellow pines growing mostly along the bases and slopes of cinder buttes and on rocky outcrops. In both areas yellow pines occur at lower and drier elevations than normal due to local edaphic factors. *P. apache* is not known to occur in typical yellow-pine forests.

Apache pocket mice may be prevented from spreading farther to the west by competition with *P. amplus*, *P. longimembris*, and *P. parvus*. There is very marginal sympatry between *P. apache* and *P. amplus* along the western edge of the range of *P. apache* in northern Arizona (Fig. 4). According to Benson (1933*b*), *P. amplus* is restricted to sand habitats in that area. In contrast, I found *P. amplus* common on rocky slopes and gravelly soils. Around Navajo Mountain, Utah, *P. longimembris* has been taken with *P. apache* (Benson, 1935). It seems likely that Apache pocket mice are prevented from occupying areas west of the Colorado River in southern Utah by competition with *P. longimembris* and *P. parvus* (Fig. 4).

South of Socorro Co., New Mexico, in the southern portion of its range (Fig. 4), *P. apache* appears to be confined to sandy hummocks and dunes in mesquite (*Prosopis*) associations. At these lower, warmer elevations, *P. apache* is very rarely captured. Here, and farther north in New Mexico and Arizona, *P. flavus* is generally most numerous on both fine-textured and gravelly soils with moderate vegetational cover. In the southern portion of the range of *P. apache,* the desert pocket mouse, *P. penicillatus,* is common in sandy areas and on creosote flats with sparse vegetational cover. Competition with *P. penicillatus* may be a major reason for the relative scarcity of *P. apache* there.

The silky pocket mouse (*P. flavus*) does not occur much farther north than the San Juan River in southeastern Utah and southwestern Colorado. North of the range of *P. flavus*, *P. apache* has been more frequently captured on non-sand substrates. This suggests that competition with *P. flavus* may generally limit *P. apache* to sandy substrates. In this regard, I found *P. flavus* to be common on loose sand soils in most areas where no *P. apache* were captured, and I caught *P. flavus* in the same trap lines as *P. apache* at just four localities.

The geographic range of *P. apache* was found to terminate at the White and Duchesne rivers in the Uintah Basin of Utah and Colorado (Fig. 5). I captured 22 *P. apache* at a single locality north of the White River (1.5 mi E Ouray). The mice were taken on hard-packed, sand-gravel conglomerate soil. There is a bridge across the White River within a kilometer of this site, and individuals may have recently colonized the north bank of the White River via the bridge. About 2 km east of this collecting site (also north of the White River), I trapped for two nights in a sand dune area extending over about 100 hectares, but caught no pocket mice. The olive-backed pocket mouse, *P. fasciatus,* was captured at several localities north of the White River, north and east of the site where I captured *P. apache* (Fig. 5). Most *P. fasciatus* were taken in sandy areas, although one was captured on a rocky slope. I did not find them to be common at any site in the Uintah Basin.

Perognathus apache and *P. fasciatus* occur in

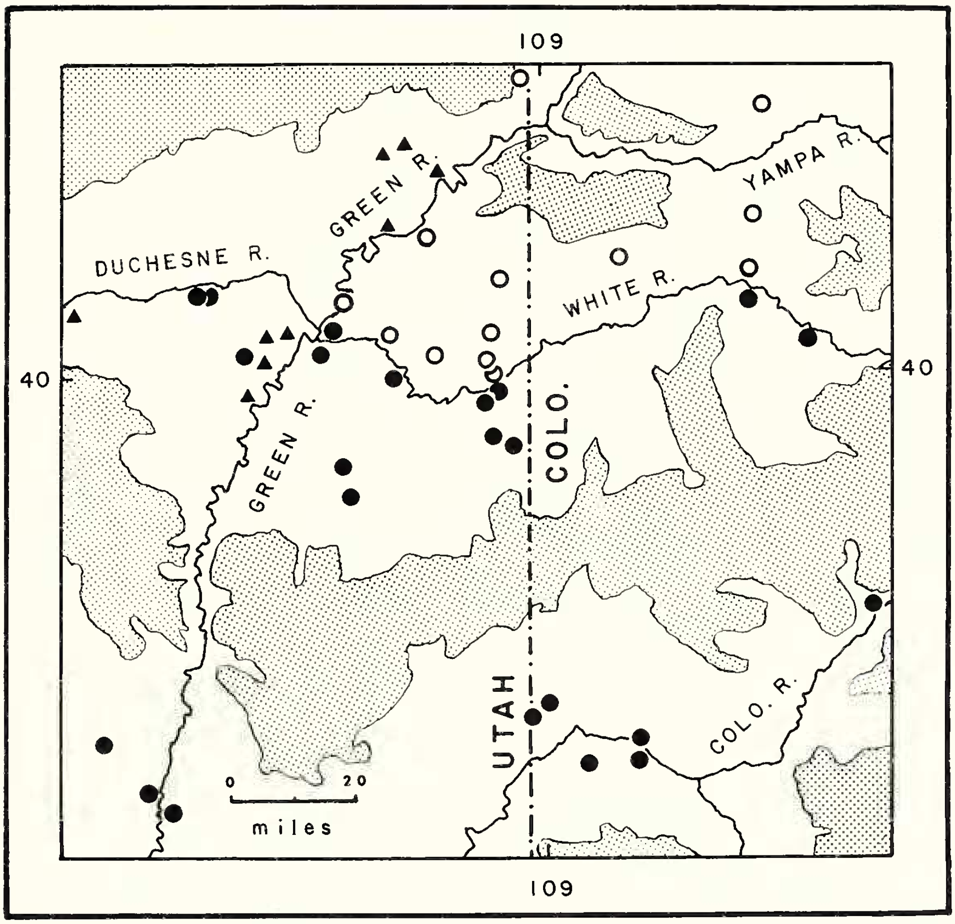

Fig. 5.—Map of northeastern Utah and northwestern Colorado, showing the distribution of three species of pocket mice. Triangles = *Perognathus parvus;* closed circles = *P. apache;* open circles = *P. fasciatus.* The shaded areas represent mountains and plateaus over 7,500 ft in elevation.

similar habitats and are nearly the same size, and it is possible that competitive exclusion limits their ranges along a line formed by the White and Duchesne rivers. Certainly the rivers are not barriers to these pocket mice, as they are shallow, and meander through broad floodplains near their confluence with the Green River. The geographic ranges of both species may be limited on the west by competition with *P. parvus* (Fig. 5). In areas where I caught *P. parvus,* they seemed to be common on all types of substrates, including slopes and level areas. There appear to be no physical barriers to the spread of *P. parvus* to the east.

All three species may be recent arrivals to the Uintah Basin, possibly within historic times. Wells (1970*a*, 1970*b*) presents evidence that both *Pinus ponderosa* and *Juniperus scopulorum* were widely distributed over the now treeless, arid Laramie Basin from at least 5,600 years B.P. to 200 years B.P. He states that the hypsithermal period (from 9,000 to 2,500 years ago) was a time of higher temperatures and greater moisture. The drastic reduction of woodlands over the past several centuries may constitute the first climatically induced episode of treelessness in the area in post-Wisconsin time, and may have allowed the recent spread of these species into the Uintah Basin.

The major habitat of Apache pocket mice extends more or less continuously from the Tavaputs Plateau of eastern Utah and adjacent Colorado southward into the Painted Desert of Arizona and the San Juan Basin of New Mexico, and southeastward into the Rio Grande Valley (Fig. 4). Most other inhabited areas are smaller, are found at higher elevations, and are more or less isolated by very narrow corridors of intermittent habitat along water courses. Populations appear to be isolated by wide stretches of unfavorable habitat in a few areas (for example, the Uintah Basin, San Luis Valley, San Augustine Plains, and Willcox Playa).

The Uintah Basin is bounded on the south by the high, east-west oriented Tavaputs Plateau (Fig. 5). Most of the plateau is over 8,000 ft. On its southern front the plateau rises abruptly, as along the Book and Roan Cliffs, and in some places is nearly 2,000 ft higher than the land to the south. On its northern side, the plateau slopes more gradually into the Uintah Basin. Sheer cliffs and steep rocky slopes on the south provide no sandy habitat for Apache pocket mice, and only a few large drainage channels cut sharply into the plateau. In Colorado, the plateau does not stand out in such bold relief, and it is possible that Apache pocket mice crossed the plateau via passes, such as that north of Rifle. More likely, however, *P. apache* colonized the Uintah Basin via the Green River Canyon through the plateau (Fig. 5). This is a narrow, precipitous route, and one that is likely to be breached only rarely.

The Rio Grande Valley abruptly narrows south of Socorro, New Mexico, and the river, from near Val Verde to near Las Cruces, flows through a narrow channel along the western front of a series of low mountains (Fig. 4). A southward drop in elevation occurs near Socorro, and creosote (*Larrea*) associations replace the more northern steppe-grasslands. Near this locality, a biotic transition occurs, and the ranges of several species characteristic of the southern desert associations end (for example, *Perognathus penicillatus*, *Geomys arenarius*, and *Peromyscus eremicus*, Findley et al., 1975). To the east, the Jornada Del Muerto (a broad, north-south valley) extends without interruption from the Deming Plains to near Val Verde. Sandy, mesquite-dominated hummocks are scattered throughout the Jornada, with creosote being found on hard-packed, fine-textured soils and on the gravelly slopes. Elevation increases gradually to the north, where the Jornada is partially blocked by a large lava flow. Sandy habitat continues intermittently northeastward in the direction of Gran Quivira, and elevation increases more rapidly. The Gran Quivira site is in a juniper association, where sands have accumulated at the base of some low hills.

The San Augustine Plains are connected on the southwest by a large drainage channel with intermittent sandy spots along its banks (Fig. 4). On the western and northwestern perimeters mountains and low hills and stretches of rocky soils probably form a barrier to dispersal and intermingling with the Rio Grande Valley population. Only low hills form the boundaries of the San Augustine Plains to the northwest, and population interchanges in the direction of Gallup and the Painted Desert are probable.

There are no significant physiographic barriers between the ranges of *P. flavescens* and *P. apache*, and their populations may be in contact at a few points. The plains pocket mouse (*P. flavescens*) may be distributed all along the Pecos River Valley, and Apache pocket mice have been collected in the upper Pecos River Valley (Fig. 4). The two populations may contact each other on the plains north of Gran Quivira, although there is a stretch of hard, rocky, limestone soils between the Pecos Valley and the Gran Quivira site. However, the most likely contact zone is in the Trans-Pecos region. Neither species is known from a fairly wide area (Fig. 4), but it is likely that Apache pocket mice occur eastward to the sands along the salt lakes west of the Guadalupe Mountains. This Trans-Pecos gap is no greater than several other gaps between known populations. That Apache pocket mice are found at nearly every sandy site within their range suggests that they have the ability to disperse through areas not suitable for supporting permanent populations. Even in areas where they are relatively abundant and widespread, such as the San Juan Basin, they are discontinuously distributed, as loose, sandy soil is a minor habitat of spotty occurrence.

INTRAPOPULATION VARIATION

Adults averaged significantly larger than subadults in most characters, and larger than juveniles in all traits except the dimensions of the permanent teeth. Consequently, juveniles and subadults were excluded from interpopulation comparisons.

There were no significant differences between the sexes of adults in the morphometric characters for the Albuquerque sample (39 males, 31 females) and the Painted Desert sample (35 males, 27 females). Females of the Uintah Basin sample (28 males, 33 females) averaged significantly larger in length of the interparietal and length of P_4. Males of the White Sands sample (28 males, 26 females) averaged significantly larger than females in bullar length, width across the bullae, and in width of M_3. All of the significant differences were relatively slight (1 to 3%) and could be due to normal sampling errors. Because of the small number of differences,

Table 3.—*Premolar cusp numbers and bullae apposition in* fasciatus *group samples.*

	P^4 cusps				P_4 cusps				Bullae meet	
Sample	1	2	4	5	2	3	4	5	Yes	No
1. *Perognathus fasciatus fasciatus*			12				12			12
2. *Perognathus fasciatus olivaceogriseus*			21			1	18			21
3. *Perognathus fasciatus litus*			19				19			18
4. *Perognathus fasciatus callistus*			31				31			31
5. *Perognathus apache* Uintah Basin		3	59	1		7	61		1	63
6. *Perognathus apache* Moab			30			1	27		1	25
7. *Perognathus apache* Painted Desert			66	1		2	66		6	55
8. *Perognathus apache* Flagstaff			36			3	34		3	30
9. *Perognathus apache* Gallup			5			2	4			6
10. *Perognathus apache* San Juan Basin			30	2		1	27	1	3	32
11. *Perognathus apache* Canyon Largo			24	5		2	23		3	27
12. *Perognathus apache* Estrella			12	3		1	13			14
13. *Perognathus apache* San Luis Valley			20			4	16			16
14. *Perognathus apache* Santa Fe			25	3		1	27		2	22
15. *Perognathus apache* Rio Grande Valley			53	18		1	54		14	57
16. *Perognathus apache* San Augustine			19			1	14			17
17. *Perognathus apache* Gran Quivira			15			1	14		2	12
18. *Perognathus apache* White Sands	1	1	52	2	7	16	28	3	7	40
19. *Perognathus apache* Deming Plains			16			2	14		4	12
20. *Perognathus flavescens copei*			14	2		2	14		5	12
Total	1	4	511	37	7	58	518	4	49	491
%	0.0	0.7	92.0	6.7	1.2	9.9	88.3	0.7	9.1	90.9

and because there was no pattern or consistency to the differences, I decided that the advantages of pooling the sexes for intersample comparisons outweighed the possible disadvantages. There were no significant differences between the sexes in the color indices. Thus, all intersample univariate and multivariate comparisons were made using pooled samples of both sexes.

Essentially no individual variation was noted in external morphology (other than normal meristic and color differences) in *P. apache, P. fasciatus,* or *P. flavescens*. Only a single specimen was found that lacked black-tipped guard hairs (MVZ 55716 from Keam's Canyon, Navajo Co., Arizona). This condition must be regarded as a rare anomaly.

Some authors (for example, Blair et al., 1957) have stated that the auditory bullae are in contact (apposed) ventrally, and have used this feature as a taxonomic character for *P. apache*. For adults, I noted if the bullae were in contact (Table 3). None of the specimens of *P. fasciatus* had bullae in apposition, whereas approximately 10% of the *P. apache* and *P. flavescens* samples had apposed bullae. The Rio Grande Valley sample exhibited a significantly greater than expected number of individuals with bullae in contact, whereas the Uintah Basin sample exhibited significantly fewer individuals than expected. Populations with relatively large bullae had a higher proportion of bullae in apposition than those with relatively small bullae, such as the Uintah Basin sample. In any case, this character is not useful as a taxonomic trait.

Several departures from the typical cusp patterns of the upper and lower fourth premolars were noted (Table 3). The normal pattern of the upper premolar consists of four major cusps, an anterior protocone (comprising the protoloph), and a three-cusped metaloph, consisting of a metacone, hypocone, and hypostyle (Fig. 6A). In about 7% of the individuals a prominent accessory cusp, representing either a paracone or a protostyle, was present on the P^4 (Fig. 6B, C, D, and F). In four individuals, the metaloph was compressed laterally, and the metaloph cusps were united into a single structure, giving the tooth a bicuspid appearance (Fig. 6E). The P^4 of one individual was unicusped (Fig. 6G).

The typical lower premolar has four prominent cusps on two transverse lophs. The anterior protolophid consists of a protoconid and protostylid, and the posterior metalophid consists of a metaconid and hypoconid (Fig. 6H). The most common departure from the normal condition was the union

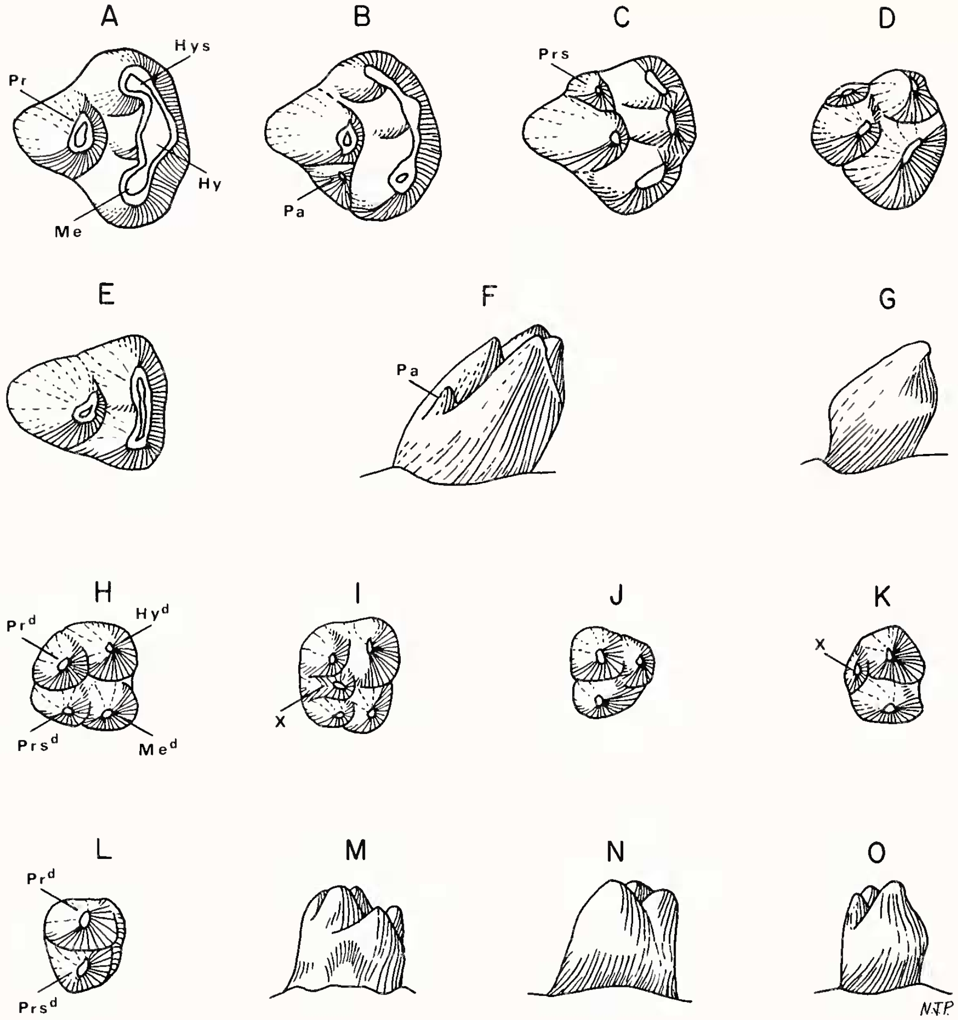

Fig. 6.—Cusp patterns and some anomalies observed in the upper and lower permanent fouth premolars of *Perognathus fasciatus* group pocket mice. A–E = occlusal views of right P^4; F and G = labial views of right P^4; H–L = occlusal views of left P_4; M–O = labial views of left P_4. A and H represent normal cusp patterns; B, C, D, F, I, K, M, and O depict teeth with accessory cusps; D, E, G, J, K, L, N, and O depict teeth with cusp deletions; B and F, I and M, J and N, and K and O each represent two views of similar anomalies. Hy = hypocone; Hy^d = hypoconid; Hys = hypostyle; Me = metacone; Me^d = metaconid; Pa = paracone; Pr = protocone; Pr^d = protoconid; Prs = protostyle; Prs^d = protostylid; X = accessory cusp of uncertain homology.

of the protostylid and metaconid into a single cusp (Fig. 6J and N). Also common was the loss of one or two of the cusps. Generally, this loss involved the cusps on the metalophid (Fig. 6K, L, and O), but in a few instances cusps on the protolophid were absent (not figured). An extra cusp of uncertain homology was noted in a few individuals (Fig. 6I, K, M, and O). Although some samples of *P. apache* exhibited a disproportionate number of cusp anomalies (for example, the White Sands and Rio Grande samples), and the samples of *P. fasciatus* exhibited fewer than expected anomalies, no obvious geographic pattern could be discerned.

INTERPOPULATION VARIATION

Karyology

The karyotypes of *P. apache*, *P. flavescens*, and *P. fasciatus* are very similar (Table 4), and widely divergent from those of other members of the subgenus *Perognathus* (Williams, 1978). A typical karyotype of *P. apache* is presented in Fig 7. The

X chromosomes of this individual (Fig. 7) were differentially contracted, a condition noted frequently in the cells of females. Other karyotypes of *P. fasciatus, P. flavescens,* and *P. apache* are figured in Williams (1978). The chromosomes of *P. flavescens copei* were identical in gross structure to all *P. apache* samples except that from near Nueva Casas Grandes, Chihuahua. This latter population differed in having a submetacentric X, and in having a pair of small biarmed autosomes. This small autosome pair appears to be homologous to the small acrocentric pair with the secondary constriction found in the other karyotypes (the pair on the right in the bottom row in Fig. 7). A single pericentric inversion can account for this difference. The karyotype of *P. fasciatus* differed from the others in having acrocentric sex chromosomes.

The nature of the karyotypic variation in the *fasciatus* group is not easy to interpret phyletically. According to one model of karyotypic evolution in the subgenus *Perognathus* (Williams, 1978), the autosomal karyotype represented by *P. fasciatus, P. flavescens,* and most *P. apache* is primitive, and the karyotype of the Casas Grandes sample is derived. The differences are slight, however, and from one to three arm additions or pericentric inversions could convert any of the karyotypes into any of the others. The submetacentric X and the acrocentric Y have been regarded as primitive for *Perognathus* (Patton, 1969; Williams, 1978), but none of these karyotypes exhibits that combination of sex chromosome structure. The identical appearance of the chromosomes of *P. flavescens* and typical *P. apache* sets them apart from *P. fasciatus* and the Casas Grandes sample of *P. apache,* but the importance of these differences has not been established.

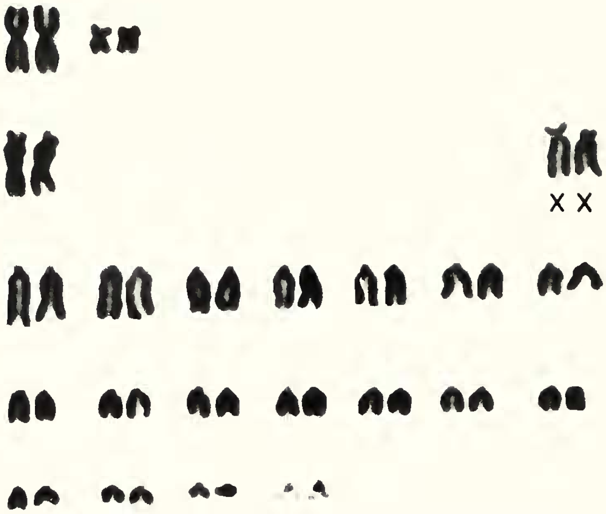

Fig. 7.—Representative karyotype of *Perognathus apache*. Female *P. a. gypsi* from Walker Ranch, White Sands National Monument, Otero Co., New Mexico.

Morphometric Variation

The statistical summaries of the standard univariate analyses are given in Table 5. Coefficients of correlation between the morphometric traits, based upon the 21 sample means, are presented in Table 6. The number of significant correlations was high, and only width of interparietals and least interbullar distance exhibited significant negative correlations with the other characters. These two traits were highly correlated ($r = 0.91$), and either expresses the degree of posterior constriction of the braincase. Some traits (TL/HBL, IPL, IPW, RW, and LID) exhibited relatively low numbers of significant correlations.

A factor analysis of the matrix of correlation demonstrated that only nine factors accounted for

Table 4.—*Chromosome characteristics of* fasciatus *group pocket mice. BA = biarmed; UA = uniarmed.*

					Autosome pairs			
Species	♂	♀	2N	FN	BA	UA	X	Y
P. fasciatus olivaceogriseus	1	1	44	48	3	18	A	A
P. fasciatus litus	1	1	44	48	3	18	A	A
P. fasciatus callistus	3	2	44	48	3	18	A	A
P. flavescens copei	5	2	44	48	3	18	ST	ST
P. apache apache	7	9	44	48	3	18	ST	ST
P. apache caryi	7	6	44	48	3	18	ST	ST
P. apache cleomophila	1	–	44	48	3	18	ST	ST
P. apache gypsi	–	1	44	48	3	18	ST	—
P. apache relictus	2	1	44	48	3	18	ST	ST
P. apache melanotis	3	1	44	50	4	17	SM	ST

Table 5.—*Standard statistics for samples of* Perognathus fasciatus, P. apache, *and* P. flavescens.

					Range						Range	
Trait	N	M	SE	CV	Minimum	Maximum	N	M	SE	CV	Minimum	Maximum
			1. *P. f. fasciatus*						2. *P. f. olivaceogriseus*			
1	11	135.7	2.269	5.54	123.0	147.0	15	133.1	1.099	3.20	126.0	142.0
2	11	62.6	1.410	7.46	57.0	70.0	15	62.7	0.720	4.45	59.0	68.0
3	11	73.1	1.504	6.82	65.0	80.0	15	70.4	0.974	5.36	65.0	81.0
4	11	17.4	0.338	6.45	16.0	19.0	15	16.7	0.157	3.63	15.7	18.0
5	11	7.5	0.157	6.92	7.0	8.0	15	7.1	0.134	7.37	6.0	8.0
6	11	0.859	0.023	8.72	0.738	0.971	15	0.894	0.016	6.92	0.738	0.985
7	8	22.60	0.208	2.59	21.65	23.50	15	22.17	0.104	1.89	21.25	22.80
8	8	22.60	0.208	2.59	21.65	23.50	15	22.14	0.101	1.77	21.25	22.75
9	10	4.88	0.063	4.08	4.55	5.20	15	4.95	0.041	3.24	4.65	5.20
10	10	3.22	0.041	4.01	3.05	3.40	15	3.12	0.032	3.96	2.95	3.35
11	8	4.41	0.063	4.04	4.05	4.70	15	4.33	0.030	2.71	4.00	4.50
12	9	7.69	0.094	3.68	7.35	8.20	15	7.60	0.086	4.39	7.00	8.05
13	8	11.92	0.082	1.96	11.45	12.20	15	11.71	0.075	2.54	11.15	12.10
14	10	2.62	0.054	6.55	2.30	2.90	15	2.63	0.062	9.18	2.30	3.00
15	10	4.69	0.104	6.99	4.25	5.20	15	4.75	0.048	3.89	4.35	5.00
16	10	8.22	0.112	4.30	7.65	8.65	15	8.20	0.073	3.45	7.55	8.65
17	10	2.21	0.028	3.94	2.10	2.35	15	2.15	0.016	2.97	2.05	2.30
18	10	3.68	0.060	5.16	3.35	3.90	15	3.74	0.041	4.30	3.40	4.00
19	8	4.80	0.052	3.04	4.65	5.10	15	4.58	0.071	6.00	4.10	5.00
20	10	2.80	0.022	2.50	2.70	2.90	15	2.78	0.024	3.38	2.60	2.95
21	11	0.63	0.007	3.51	0.61	0.68	15	0.62	0.006	3.65	0.58	0.65
22	11	0.67	0.011	5.32	0.61	0.74	15	0.67	0.010	5.60	0.61	0.71
23	10	0.62	0.006	3.29	0.58	0.65	15	0.61	0.008	4.85	0.58	0.65
24	10	0.73	0.014	5.89	0.68	0.81	15	0.72	0.010	5.26	0.68	0.81
25	11	2.76	0.070	8.24	2.40	3.05	15	2.75	0.033	4.60	2.40	2.90
26	11	0.98	0.010	3.39	0.90	1.03	15	1.00	0.014	5.31	0.90	1.10
27	11	1.10	0.022	6.58	1.00	1.23	15	1.09	0.015	5.27	0.97	1.19
28	10	0.71	0.013	5.82	0.65	0.77	15	0.70	0.009	4.96	0.65	0.77
29	11	0.86	0.014	5.48	0.81	0.97	15	0.86	0.008	3.70	0.81	0.90
30	11	0.98	0.008	2.69	0.94	1.00	15	0.97	0.006	2.34	0.94	1.03

90% of the total variance, and that the first five factors accounted for 85.1% of the variance (Table 7). Each of the traits except length and width of the interparietals and least interbullar distance showed high positive loading on Factor I, which is a general size factor. The posterior cranial region become more constricted with increasing size, as demonstrated by the negative loading of interparietal dimensions and least interbullar distance on Factor I.

Factor II, which accounts for 15.6% of the total variance, showed high positive values for width of interparietals, least interbullar distance, width of P_4, and width of M^3. Traits with high negative values were least interorbital breadth, length of M_1, and length of hind foot. Factor II was most strongly influenced by traits expressing the postcranial constriction.

Factor III, accounting for 5.7% of the total variance, showed a high positive value only for length of interparietal. Width of interparietals also also exhibited positive loading for Factor III, whereas length of tail exhibited negative loading. Samples with high positive scores for Factor III had relatively long interparietals and short tails. Factor IV accounted for 4.2% of the total variance and was loaded most strongly by length of articular process. Factor V, accounting for 3.5% of the total variance, had high loading on the TL/HBL ratio. Negative loading on length of head and body and positive loading on length of tail also reflect this "tail factor." Samples with high factor scores for Factor V had relatively long tails. Beyond Factor V, the individual factors accounted for relatively little of the variance.

The factor scores of the first three factors, for each of the samples, are plotted in Fig. 8. Note that *P. fasciatus* samples are most distinctive in terms of Factor II, having wide interparietals and narrow

Table 5.—*Continued.*

Trait	N	M	SE	CV	Range		N	M	SE	CV	Range	
					Minimum	Maximum					Minimum	Maximum
			3. *P. f. litus*						4. *P. f. callistus*			
1	27	139.8	0.824	3.06	134.0	149.0	18	134.3	1.249	3.95	123.0	146.0
2	27	66.9	0.536	4.16	61.0	75.0	18	63.3	1.105	7.41	53.0	70.0
3	27	72.9	0.531	3.78	69.0	80.0	18	71.0	0.925	5.53	63.0	78.0
4	27	17.7	0.099	2.89	16.9	19.0	18	18.0	0.164	3.88	17.0	19.0
5	27	6.9	0.093	6.98	6.1	7.9	18	6.8	0.200	12.47	5.0	8.0
6	27	0.919	0.009	5.02	0.813	1.029	18	0.894	0.022	10.58	0.739	1.079
7	27	23.23	0.118	2.64	22.15	24.80	17	23.00	0.111	1.98	21.95	24.00
8	27	23.07	0.111	2.50	22.10	24.55	17	22.85	0.102	1.85	21.90	23.70
9	27	5.13	0.026	2.65	4.95	5.40	18	5.18	0.028	2.34	5.00	5.40
10	27	3.27	0.019	3.03	3.05	3.50	18	3.18	0.026	3.50	3.00	3.40
11	27	4.45	0.022	2.69	4.15	5.65	18	4.44	0.027	2.65	4.20	4.60
12	27	8.60	0.056	3.39	8.00	9.35	18	8.48	0.062	3.11	7.90	8.90
13	27	12.90	0.072	2.81	12.20	13.85	18	12.71	0.081	2.62	12.10	13.35
14	27	2.63	0.040	8.01	2.25	3.15	18	2.78	0.057	8.67	2.25	3.35
15	27	4.50	0.072	8.36	3.85	5.15	18	4.56	0.054	5.19	4.15	5.15
16	27	8.55	0.051	3.11	7.95	9.10	17	8.30	0.072	3.58	7.75	8.85
17	27	2.33	0.021	4.69	2.10	2.55	17	2.23	0.029	5.30	2.05	2.45
18	27	3.71	0.027	3.76	3.50	4.00	18	3.64	0.024	2.81	3.45	3.85
19	27	4.37	0.077	9.13	3.55	5.30	18	4.39	0.080	7.78	3.65	5.05
20	27	2.84	0.014	2.69	2.65	2.95	16	2.82	0.026	3.65	2.60	3.00
21	27	0.66	0.006	4.75	0.61	0.71	14	0.64	0.004	2.37	0.61	0.65
22	27	0.69	0.005	4.15	0.65	0.77	14	0.67	0.013	7.10	0.61	0.74
23	27	0.60	0.007	5.71	0.55	0.68	14	0.62	0.008	5.07	0.58	0.68
24	27	0.74	0.007	5.01	0.65	0.81	14	0.72	0.006	3.25	0.68	0.74
25	27	2.89	0.025	4.57	2.53	3.20	14	2.86	0.037	4.87	2.67	3.13
26	27	1.03	0.008	3.90	0.97	1.10	14	1.00	0.008	2.95	0.97	1.03
27	27	1.10	0.009	4.06	1.00	1.19	14	1.10	0.012	3.95	1.03	1.16
28	27	0.71	0.008	6.18	0.61	0.81	14	0.73	0.012	5.94	0.68	0.81
29	27	0.91	0.010	5.92	0.81	1.00	14	0.88	0.009	3.91	0.84	0.94
30	27	0.95	0.007	3.98	0.87	1.00	14	0.96	0.015	5.81	0.81	1.03

interorbital regions. The *P. flavescens* samples are most notable in their highly negative scores for Factor I and high positive scores for Factor III. They are small in size (Factor I), with relatively short tails and with broad interparietals (Factor III). Of the *P. apache* samples, the northern ones are, perhaps, the most unique, being large, with long tails and narrow crania (Factor I). This is, of course, a simplification of the geographic variation in the morphometric traits (Table 5), but most of the variation (77.4%) is accounted for in these three factors, and the factors are most strongly influenced by suites of related characters.

Tests for significant differences between samples, using the SS-STP routine, resulted in a large number of superfluous comparisons between samples that are widely separated geographically. Therefore, only a summary of the comparisons between samples in geographic proximity is presented (Table 8). The comparisons were limited to samples of populations that are neighbors and, potentially, can exchange genes. The results of the SS-STP comparisons are illustrated in Fig. 9. To simplify the picture, some of the less likely comparisons were omitted from Fig. 9, but are given in Table 8. Note that the *P. fasciatus* samples (1–4) exhibited high numbers of significant differences with adjacent samples of *P. flavescens* (21) and *P. apache* (5). These were not the highest numbers of significant differences, but because these populations are sympatric, or, in the case of *P. apache*, in close proximity, reproductive isolation is suggested. Of the *P. apache* samples, numbers 5, 6, 10, 12, 15, 16 or 17, and 19 form a chain of populations with few significant differences, extending from northern Utah to Chihuahua (Fig. 9). Most other samples peripheral to this chain are connected by only one or a few routes. For example, the Painted Desert and Flag-

Table 5.—*Continued.*

					Range						Range	
Trait	N	M	SE	CV	Minimum	Maximum	N	M	SE	CV	Minimum	Maximum
	5. *P. apache* Uintah Basin						6. *P. apache* Moab					
1	60	140.7	0.717	3.94	128.0	155.0	27	137.4	1.078	4.07	123.0	146.0
2	60	68.3	0.489	5.55	52.0	74.0	27	66.7	0.817	6.36	59.0	73.0
3	61	72.5	0.646	6.97	61.0	87.0	27	70.7	0.636	4.68	64.0	78.0
4	61	18.2	0.095	4.08	16.7	20.0	27	18.5	0.233	6.56	15.0	21.0
5	60	7.0	0.064	7.05	6.0	8.0	24	6.7	0.107	7.79	6.0	8.0
6	60	0.949	0.012	9.67	0.667	1.147	27	0.946	0.013	7.37	0.815	1.078
7	60	23.92	0.076	2.44	22.85	25.50	23	23.53	0.133	2.71	22.30	24.60
8	59	23.74	0.075	2.42	22.55	25.30	21	23.33	0.127	2.49	22.05	24.25
9	61	5.36	0.023	3.36	5.00	5.70	25	5.26	0.030	2.85	5.00	5.60
10	61	3.30	0.015	3.61	3.05	3.55	27	3.27	0.048	7.64	2.35	3.75
11	61	4.58	0.017	2.83	4.35	4.90	26	4.51	0.028	3.19	4.15	4.75
12	61	8.80	0.038	3.36	8.30	9.45	26	8.51	0.051	3.08	7.85	9.05
13	61	13.08	0.042	2.50	12.45	14.00	24	12.81	0.058	2.24	12.30	13.25
14	61	3.22	0.028	6.71	2.80	3.65	26	3.14	0.037	5.95	2.80	3.50
15	61	4.35	0.034	6.07	3.75	4.95	26	4.39	0.085	9.92	3.80	5.25
16	60	8.74	0.044	3.92	8.00	9.50	25	8.54	0.075	4.38	7.90	9.25
17	60	2.23	0.014	4.90	2.00	2.50	25	2.30	0.024	5.33	2.00	2.60
18	61	3.85	0.019	3.88	3.60	4.20	26	3.79	0.043	5.79	3.45	4.30
19	61	3.94	0.027	5.27	3.50	4.35	25	4.05	0.069	8.49	3.55	4.60
20	60	2.95	0.011	2.88	2.70	3.10	27	2.93	0.019	3.39	2.70	3.10
21	60	0.65	0.004	4.91	0.58	0.71	27	0.63	0.007	6.26	0.52	0.68
22	60	0.66	0.004	4.23	0.61	0.71	27	0.64	0.008	6.75	0.58	0.71
23	60	0.64	0.004	4.74	0.58	0.71	27	0.64	0.006	5.28	0.58	0.71
24	60	0.75	0.005	4.61	0.68	0.84	27	0.74	0.009	6.36	0.65	0.81
25	60	2.84	0.022	6.00	2.53	3.27	27	2.96	0.038	6.65	2.67	3.40
26	61	1.05	0.005	4.00	0.94	1.16	27	1.03	0.006	3.05	1.00	1.10
27	61	1.22	0.005	3.37	1.13	1.32	27	1.20	0.009	3.98	1.10	1.29
28	61	0.72	0.005	5.70	0.61	0.77	26	0.69	0.008	6.20	0.61	0.77
29	60	0.96	0.005	3.60	0.84	1.06	27	0.99	0.007	3.91	0.94	1.06
30	60	1.01	0.005	4.11	0.94	1.13	27	1.01	0.010	5.28	0.87	1.13

staff samples were closely similar, and appear to be linked with the others along an avenue to the east, in the direction of the Gallup sample (Fig. 9). The Canyon Largo sample from higher juniper and pinyon-juniper associations (11), was very distinct from the adjacent San Juan Basin sample (10) from a lower, sage-grassland habitat. The Canyon Largo sample was more similar to the Santa Fe (14) and Estrella samples (12) from ecologically similar areas.

The Rio Grande Valley sample (15) was very different from the adjacent Deming Plains sample (19), and they appear to be linked only by an indirect route through the Gran Quivira (17) or San Augustine Plains sample (16). Mice typical of the Rio Grande Valley sample were found from the Rio Salado, north of Albuquerque, southward to where the Valley narrows near Val Verde, New Mexico. No Apache pocket mice are known from between Val Verde and Las Cruces in the Rio Grande Valley. I have, however, collected a few Apache pocket mice, typical of the Deming Plains population, as far north as Engle in the Jornada del Muerto.

Only two significant differences were found between the Deming Plains sample of *P. apache* and *P. flavescens copei* (Table 8, Fig. 9). Other populations of the Apache pocket mouse in proximity to *P. flavescens* were quite distinct from *flavescens*, with from seven to 16 significant differences. These were no greater than the differences among some samples of Apache pocket mice, however. Of the potential avenues of gene exchange between Apache and plains pocket mice, the Trans-Pecos route seems most likely on the basis of the univariate analyses (Fig. 9).

Even though the Uintah Basin appears to be isolated, samples of the Apache pocket mice occupying the Basin were essentially the same as samples

Table 5.—*Continued.*

Trait	N	M	SE	CV	Range		N	M	SE	CV	Range	
					Minimum	Maximum					Minimum	Maximum
		7. *P. apache* Painted Desert						8. *P. apache* Flagstaff				
1	52	133.1	0.987	5.26	119.0	156.0	32	132.2	1.098	4.69	120.0	145.0
2	52	64.1	0.595	6.64	50.0	73.0	32	63.4	0.598	5.34	58.0	73.0
3	54	69.3	0.750	7.78	61.0	89.0	32	68.8	0.724	5.95	58.0	77.0
4	54	18.5	0.119	4.97	17.0	21.0	32	19.1	0.137	4.05	17.5	20.5
5	28	6.1	0.067	8.15	6.0	7.0	7	6.4	0.190	7.86	6.0	7.0
6	52	0.929	0.012	9.49	0.714	1.076	32	0.918	0.011	6.73	0.824	1.086
7	49	22.60	0.090	2.90	21.30	24.35	31	22.60	0.156	3.83	21.10	24.55
8	49	22.42	0.089	2.89	21.25	23.95	32	22.50	0.149	3.73	21.00	24.50
9	51	5.14	0.022	3.07	4.75	5.55	32	5.25	0.039	4.18	4.80	5.70
10	55	3.19	0.022	5.07	2.95	3.85	32	3.19	0.028	4.99	2.85	3.60
11	53	4.37	0.021	3.58	4.05	4.65	32	4.29	0.029	3.83	3.95	4.60
12	54	8.37	0.049	4.41	7.50	9.35	32	7.97	0.071	5.02	7.25	8.60
13	49	12.58	0.059	3.29	11.65	13.35	31	12.25	0.076	3.49	11.60	13.15
14	54	2.87	0.032	8.01	2.20	3.30	32	2.88	0.041	8.02	2.35	3.40
15	54	3.94	0.040	7.26	3.30	4.65	32	3.92	0.073	10.50	2.80	4.70
16	53	7.94	0.048	4.55	7.10	8.95	32	8.15	0.070	4.87	7.40	9.25
17	51	2.26	0.016	5.30	2.05	2.55	32	2.32	0.024	5.94	2.10	2.60
18	55	3.68	0.023	4.61	3.35	4.15	32	3.69	0.028	4.24	3.40	4.00
19	53	3.90	0.034	6.06	3.45	4.45	31	3.87	0.057	8.21	3.10	4.40
20	55	2.79	0.014	2.07	2.60	3.05	32	2.76	0.021	4.13	2.50	3.05
21	55	0.58	0.006	7.33	0.48	0.65	32	0.59	0.008	7.64	0.48	0.68
22	55	0.62	0.006	6.94	0.55	0.74	32	0.60	0.007	6.43	0.55	0.68
23	55	0.61	0.005	6.17	0.55	0.68	32	0.61	0.007	6.68	0.52	0.68
24	55	0.70	0.006	6.90	0.61	0.81	32	0.70	0.008	6.25	0.61	0.81
25	54	2.80	0.002	5.80	2.33	3.20	32	2.86	0.030	5.99	2.53	3.27
26	55	0.99	0.006	4.68	0.87	1.10	32	0.97	0.007	4.36	0.87	1.03
27	55	1.10	0.008	5.63	0.94	1.26	32	1.10	0.011	5.56	0.97	1.23
28	54	0.65	0.006	7.41	0.55	0.81	32	0.66	0.008	7.33	0.55	0.81
29	55	0.93	0.007	5.35	0.81	1.06	32	0.95	0.009	5.31	0.84	1.06
30	53	0.96	0.007	5.34	0.84	1.13	32	0.94	0.009	5.41	0.84	1.03

of populations from farther south in Utah and Colorado. On the other hand, the San Luis Valley population of south-central Colorado appeared to be relatively isolated and well differentiated from its neighbors. Samples of the Painted Desert and Flagstaff populations were quite different from those from adjacent areas to the north and east. The lower San Juan River and Chuska Mountains appear to be effective barriers to gene exchange between these populations (Fig. 4).

The most apparent geographic pattern to the morphometric variation in Apache pocket mice was a strong north-south size cline. This is best seen in the main chain of populations extending from north to south. Occipitonasal length is representative of size and well illustrates this cline (Fig. 10). A correlation analysis between the morphometric characters and the climatic and geographic variables showed the size cline to be highly significant (Table 9, Fig. 11). Latitude showed 23 significant positive correlations with the morphometric traits, of which 21 were highly significant (Table 9). The climatic severity index, growing season, and mean July minimum temperature were not significantly correlated with any of the morphometric traits. Mean annual temperature was negatively correlated with body size (TOTL and HBL). Latitude was, however, more highly correlated with size than the variables expressing environmental temperature. It is probable that these variables do not adequately express the complexities of the yearly climatic cycle or the temperature factors affecting these pocket mice. Apache pocket mice do vary in size as predicted by Bergman's principle, and it is most likely that relative heat loss is an important factor in determining size in these populations. These mice store seeds, become hypothermic at low ambient temperatures and in times of food deprivation, and are generally

Table 5.—*Continued.*

Trait	N	M	SE	CV	Range		N	M	SE	CV	Range	
					Minimum	Maximum					Minimum	Maximum
			9. *P. apache* Gallup						10. *P. apache* San Juan Basin			
1	8	131.5	2.062	4.43	124.0	139.0	32	137.8	1.093	4.49	127.0	151.0
2	8	61.9	1.187	5.42	58.0	69.0	32	67.3	0.511	4.29	62.0	72.0
3	8	69.6	1.557	6.33	63.0	76.0	32	70.4	0.747	6.00	63.0	80.0
4	8	18.3	0.164	2.53	18.0	19.0	32	19.5	0.105	3.06	18.0	20.0
5	0	—	—	—	—	—	32	6.8	0.050	4.19	6.0	7.0
6	8	0.891	0.025	7.85	0.815	0.985	32	0.958	0.009	5.20	0.858	1.078
7	5	22.54	0.206	2.05	22.00	23.00	32	23.34	0.135	3.27	21.30	24.70
8	6	22.41	0.183	2.00	21.80	23.00	32	23.14	0.128	3.12	21.10	24.60
9	6	5.16	0.077	3.65	4.90	5.35	32	5.29	0.033	3.55	4.90	5.65
10	6	3.29	0.042	3.10	3.10	3.35	32	3.42	0.025	4.09	3.15	3.75
11	6	4.37	0.031	1.72	4.30	4.45	32	4.40	0.019	2.41	4.20	4.60
12	5	8.17	0.087	2.35	7.90	8.40	32	8.42	0.067	4.45	7.60	9.25
13	6	12.51	0.073	1.55	12.25	12.80	32	12.71	0.062	2.81	12.05	13.70
14	6	3.19	0.104	8.01	2.80	3.45	32	3.07	0.047	2.65	3.70	8.76
15	6	4.07	0.077	4.64	3.75	4.25	32	4.05	0.057	8.02	3.50	4.75
16	6	8.14	0.104	3.14	7.80	8.50	32	8.46	0.075	5.01	7.60	9.25
17	6	2.26	0.047	5.13	2.10	2.40	30	2.38	0.026	5.88	1.90	2.60
18	6	3.71	0.108	7.16	3.40	4.00	32	3.85	0.034	5.00	3.50	4.30
19	6	4.01	0.030	1.83	3.90	4.10	32	3.92	0.043	6.26	3.35	4.40
20	7	2.88	0.031	2.81	2.75	3.00	32	2.97	0.017	3.31	2.75	3.15
21	7	0.62	0.011	4.70	0.58	0.65	32	0.62	0.007	6.65	0.55	0.71
22	7	0.63	0.011	4.53	0.61	0.68	32	0.65	0.008	6.98	0.58	0.77
23	7	0.63	0.009	4.02	0.58	0.65	32	0.64	0.007	5.88	0.58	0.74
24	7	0.73	0.018	6.70	0.68	0.81	32	0.75	0.009	7.10	0.68	0.87
25	7	2.77	0.095	9.09	2.27	3.00	32	2.93	0.027	5.28	2.60	3.33
26	5	0.99	0.012	2.72	0.97	1.03	32	1.05	0.008	4.49	0.97	1.13
27	5	1.13	0.016	3.11	1.10	1.16	32	1.18	0.007	3.17	1.10	1.26
28	4	0.68	0.022	6.73	0.61	0.71	32	0.69	0.007	6.01	0.61	0.77
29	7	0.99	0.010	2.45	0.97	1.03	32	0.99	0.007	4.08	0.94	1.10
30	7	0.99	0.013	3.62	0.94	1.03	32	1.01	0.009	4.84	0.90	1.13

inactive on the surface during inclement weather (personal observations); so it would, perhaps, be naive to expect a simple relationship between size and mean annual temperature.

Another factor that is possibly working in concert with temperature in selecting for size is differential resource allocation. In the southern portion of their range, Apache pocket mice are sympatric with another sand-dwelling species, *P. penicillatus*. The desert pocket mouse has about the same body size as the northern populations of *P. apache* (HBL = 70–75 mm), but is about 13% larger than the sympatric population of *P. apache*. Mares and Williams (1977) presented experimental evidence suggesting that the differences in body size among several heteromyid granivores determines, in part, the sizes of the seeds gathered. They also showed that larger species were able to gather a greater size array of seeds. Thus, within limits, larger body size should be advantageous for most species. Competition between *P. apache* and *P. penicillatus* could select for mice with well-differentiated body sizes, and could be partly responsible for the small size of southern populations of *P. apache*. North of the range of *P. penicillatus*, the lack of competition with that species may permit selection for larger body size in *P. apache*. North of the San Juan River, the absence of competition with sympatric congeners and cooler ambient temperatures may both be important factors in the selection for even larger body size in Apache pocket mice.

The size of the auditory bullae (BL, BW) and interorbital breadth exhibited significant negative correlations with mean annual precipitation (Table 9, Fig. 12). These traits were positively correlated with latitude, although latitude and mean annual

Table 5.—*Continued.*

Trait	N	M	SE	CV	Range		N	M	SE	CV	Range	
					Minimum	Maximum					Minimum	Maximum
		11. *P. apache* Canyon Largo						12. *P. apache* Estrella				
1	25	132.9	1.171	4.48	120.0	143.0	13	137.4	1.146	3.01	131.0	144.0
2	25	63.6	0.716	5.63	55.0	71.0	13	67.6	0.738	3.94	62.0	72.0
3	26	69.0	0.860	6.35	57.0	75.0	13	69.8	0.856	4.42	64.0	75.0
4	26	17.8	0.126	3.61	16.7	19.3	13	19.3	0.166	3.11	18.5	20.5
5	26	6.6	0.062	4.76	6.1	7.2	13	6.7	0.104	5.64	6.0	7.0
6	25	0.922	0.015	8.25	0.733	1.105	13	0.970	0.015	5.74	0.837	1.045
7	24	22.57	0.162	3.53	21.35	24.10	13	23.05	0.161	2.53	22.25	23.80
8	25	22.41	0.151	3.37	21.30	24.00	13	22.87	0.168	2.63	22.00	23.70
9	26	5.13	0.034	3.46	4.75	5.50	13	5.22	0.051	3.53	5.00	5.50
10	26	3.26	0.034	5.26	2.85	3.50	13	3.34	0.024	3.20	3.50	2.67
11	26	4.32	0.027	3.22	4.10	4.65	13	4.36	0.038	3.18	4.15	4.65
12	24	7.97	0.065	4.02	7.45	8.55	13	8.30	0.038	4.25	7.65	8.80
13	25	12.27	0.080	3.34	11.65	13.20	13	12.75	0.096	2.59	12.10	13.25
14	26	2.81	0.043	7.84	2.30	3.20	13	2.89	0.059	7.45	2.60	3.30
15	26	3.96	0.045	5.87	3.60	4.45	13	4.09	0.069	6.06	3.55	4.45
16	25	8.08	0.071	4.42	7.55	9.00	13	8.27	0.107	4.67	7.60	8.80
17	25	2.23	0.030	6.83	1.85	2.40	13	2.31	0.039	6.13	2.10	2.50
18	26	3.68	0.039	5.39	3.35	4.10	13	3.79	0.045	4.32	3.55	4.10
19	26	3.85	0.054	7.20	3.40	4.30	13	3.96	0.064	5.83	3.50	4.25
20	25	2.85	0.030	5.30	2.55	3.15	13	2.93	0.033	4.04	2.80	3.15
21	25	0.59	0.011	9.14	0.52	0.68	13	0.63	0.008	4.49	0.58	0.68
22	25	0.63	0.008	6.75	0.55	0.71	13	0.64	0.011	6.30	0.58	0.74
23	25	0.63	0.008	6.48	0.55	0.68	13	0.62	0.011	6.58	0.55	0.68
24	25	0.74	0.009	6.34	0.65	0.84	13	0.74	0.013	6.40	0.68	0.84
25	24	2.88	0.036	6.13	2.67	3.20	13	2.90	0.017	4.36	2.67	3.13
26	26	1.01	0.011	5.70	0.94	1.13	13	1.02	0.013	4.78	0.97	1.10
27	26	1.13	0.010	4.58	1.00	1.19	13	1.14	0.014	4.38	1.03	1.19
28	26	0.68	0.007	5.29	0.61	0.74	13	0.67	0.011	6.11	0.58	0.74
29	25	0.95	0.010	5.43	0.81	1.03	13	0.97	0.009	3.60	0.90	1.03
30	25	0.98	0.011	5.84	0.87	1.10	13	0.99	0.011	3.90	0.90	1.03

precipitation were not correlated (Table 10). Relative bullar size appears to be related to two independent factors, the general size factor and the amount of environmental moisture. These two factors were not correlated, and their associations with bullar and interorbital size were conflicting. Variation in the size of the auditory bullae is in agreement with the commonly observed ecogeographic principle of animals from drier climates having larger sound sensing organs that their relatives from moister climates. The rostrum (NL, NW, RW, IOB) was wider and longer in samples from the more arid localities, but only interorbital breadth showed a significant negative correlation with mean annual precipitation. This association is as one would expect if these mice are adapted to decrease pulmonary water loss in drier climates. The strong size cline, however, partially masked these associations.

Tail size did not exhibit a significant negative correlation with mean annual temperature, contrary to the prediciton of Allen's principle. Rather, the TL/HBL ratio increased with increasing latitude (r = 0.60), with increasing body size (r with HBL = 0.68) and with head size (r with ONL = 0.72). This suggests that some factor or factors are selecting for increasingly longer tails with increasing body size. I have observed these mice in bipedal stances while foraging, and a longer tail could be necessary to counterbalance a larger body. The relationship between head size and tail length is shown in Fig. 13.

The significant associations between length of interparietal and elevation, and between certain dental measurements (P^4W and M_1L; Table 9) and elevation adjusted for latitude have no obvious explanations. Perhaps they are spurious correla-

Table 5.—*Continued.*

					Range						Range	
Trait	N	M	SE	CV	Minimum	Maximum	N	M	SE	CV	Minimum	Maximum
	13. *P. apache* San Luis Valley						14. *P. apache* Santa Fe					
1	17	136.3	1.288	3.90	123.0	144.0	24	136.2	1.325	4.81	118.0	145.0
2	17	67.2	0.671	4.11	60.0	71.0	24	65.0	0.797	6.01	56.0	70.0
3	17	69.1	0.813	4.85	63.0	76.0	26	70.2	0.797	5.78	62.0	80.0
4	17	18.6	0.139	3.09	18.0	20.0	26	18.2	0.141	3.95	16.5	20.0
5	15	6.7	0.152	8.86	6.0	8.0	11	6.6	0.187	9.38	5.8	7.8
6	17	0.972	0.011	4.58	0.882	1.031	24	0.927	0.013	7.15	0.802	1.060
7	13	22.41	0.186	3.00	21.00	23.60	22	22.46	0.136	2.85	21.25	24.20
8	15	22.39	0.162	2.80	21.00	23.55	21	22.40	0.138	2.82	21.25	23.90
9	16	5.37	0.045	3.39	5.00	5.65	24	5.10	0.034	3.27	4.80	5.40
10	17	3.12	0.030	3.97	2.90	3.35	26	3.24	0.024	3.80	3.00	3.55
11	16	4.21	0.029	2.78	3.95	4.35	25	4.34	0.030	3.50	4.10	4.60
12	14	7.86	0.074	3.52	7.30	8.30	25	7.73	0.066	4.27	7.00	8.45
13	15	12.14	0.080	2.58	11.60	12.50	23	12.17	0.087	3.38	11.55	13.55
14	16	2.63	0.048	7.30	2.35	3.00	24	2.81	0.059	10.25	2.35	3.55
15	16	3.83	0.065	6.81	3.35	4.50	24	4.06	0.078	9.44	3.25	4.90
16	16	7.79	0.098	5.02	7.15	8.40	25	8.07	0.064	4.02	7.35	8.65
17	15	2.25	0.027	4.70	2.05	2.35	24	2.24	0.028	6.16	1.95	2.50
18	15	3.75	0.041	4.29	3.45	3.95	25	3.74	0.038	5.13	3.35	4.10
19	15	3.99	0.052	5.01	3.65	4.40	24	4.15	0.056	6.63	3.75	4.75
20	16	2.76	0.027	3.93	2.55	2.90	27	2.81	0.017	3.24	2.65	2.95
21	16	0.57	0.010	7.27	0.48	0.65	27	0.61	0.006	5.32	0.55	0.68
22	16	0.59	0.006	4.38	0.55	0.65	27	0.64	0.006	5.05	0.58	0.71
23	16	0.61	0.007	4.71	0.55	0.65	27	0.61	0.007	5.65	0.55	0.68
24	16	0.71	0.009	5.12	0.68	0.81	27	0.73	0.007	5.19	0.65	0.81
25	16	2.78	0.021	6.36	2.40	3.07	27	2.73	0.030	5.75	2.40	3.00
26	16	0.86	0.008	3.66	0.81	0.90	26	0.97	0.011	5.93	0.89	1.06
27	16	1.02	0.010	3.77	0.97	1.10	26	1.11	0.010	4.80	1.00	1.19
28	16	0.63	0.008	5.22	0.58	0.71	26	0.65	0.008	6.19	0.55	0.74
29	16	0.95	0.008	3.26	0.90	1.00	27	0.95	0.007	3.67	0.87	1.00
30	16	0.94	0.009	3.73	0.90	1.03	27	0.97	0.008	4.34	0.90	1.06

tions, or perhaps they are somehow affected by available moisture which increases with increasing elevation.

Color Variation

Color was more variable geographically than were the morphometric traits, and consequently, I did not group samples as much for the analysis of color. Table 11 lists the means for the color indices of samples of *P. apache* and *P. flavescens*. In general, an increase in darkness was accompanied by an increase in richness ($r = 0.52$). Notable exceptions were seen in samples from unusually light or dark colored soils. The Uintah Basin sample had a relatively large number of black-tipped guard hairs (darkness), but the yellowish color (richness) was quite pale. Soils in that region are very pale-tannish or grayish in color. The White Sands sample was also exceptional in that yellowish pigment was absent in most adults (most young mice in juvenile pelage had a very pale yellowish tinge). Their basic color was white, overlain by a normal number of black-tipped hairs, presenting a neutral, grayish appearance. The gypsum dunes upon which these mice were collected are white. Samples from reddish sands, such as those near Caprock and Tolar were darker and more orange-colored than those from tanner soils.

A correlation analysis between the color parameters and the climatic and geographic variables is given in Table 10. The color indices were all highly correlated with mean annual precipitation, and richness and relative darkness were correlated with elevation (elevation and mean annual precipitaion were highly correlated). The relative darkness index is plotted against mean annual precipitation in

Table 5.—*Continued.*

					Range						Range	
Trait	N	M	SE	CV	Minimum	Maximum	N	M	SE	CV	Minimum	Maximum
	15. *P. apache* Rio Grande Valley						16. *P. apache* San Augustine Plains					
1	66	133.8	0.762	4.77	119.0	151.0	17	128.8	1.651	5.28	117.0	145.0
2	66	63.1	0.565	7.32	50.0	78.0	17	60.2	1.034	7.08	51.0	68.0
3	68	70.9	0.506	6.00	58.0	80.0	17	68.6	0.955	5.74	64.0	77.0
4	68	18.6	0.100	4.62	17.0	20.0	17	18.1	0.157	3.59	17.3	19.5
5	67	6.6	0.067	8.39	5.0	8.0	14	6.6	0.093	5.34	6.1	7.1
6	66	0.892	0.011	9.64	0.734	1.121	17	0.879	0.015	7.08	0.708	0.984
7	63	22.88	0.087	3.14	21.00	24.45	15	22.30	0.131	2.27	21.75	23.60
8	63	22.81	0.085	3.06	21.00	24.15	15	22.20	0.124	2.16	21.65	23.45
9	68	5.24	0.026	4.12	4.65	5.75	17	5.09	0.053	4.32	4.75	5.60
10	69	3.27	0.017	4.41	3.00	3.60	17	3.15	0.029	3.83	2.95	3.35
11	68	4.36	0.016	3.14	4.05	4.65	17	4.28	0.025	2.38	4.05	4.45
12	64	8.10	0.045	4.60	7.30	8.95	16	7.97	0.073	3.68	7.50	8.40
13	64	12.34	0.059	3.79	11.35	13.40	17	12.24	0.089	2.97	11.60	12.90
14	68	2.87	0.027	7.80	2.35	3.35	17	2.81	0.060	8.79	2.40	3.35
15	68	4.07	0.039	7.93	3.45	5.00	17	4.09	0.081	8.17	3.50	4.65
16	65	8.28	0.046	4.51	7.35	9.15	15	7.95	0.072	3.49	7.60	8.55
17	66	2.28	0.020	7.02	1.95	2.80	16	2.14	0.022	4.11	2.00	2.30
18	68	3.78	0.028	6.20	3.30	4.25	17	3.71	0.047	5.31	3.50	4.15
19	68	3.99	0.040	8.19	2.65	5.10	17	4.00	0.079	8.11	3.45	4.50
20	69	2.85	0.013	3.85	2.60	3.20	17	2.74	0.025	3.81	2.55	2.90
21	69	0.58	0.005	6.91	0.52	0.71	17	0.58	0.010	6.80	0.52	0.65
22	69	0.64	0.004	6.03	0.58	0.71	17	0.60	0.009	5.81	0.55	0.68
23	69	0.61	0.004	5.88	0.52	0.71	17	0.60	0.009	6.07	0.52	0.68
24	69	0.73	0.005	5.41	0.61	0.81	17	0.71	0.011	6.37	0.65	0.84
25	69	2.82	0.010	6.05	2.40	3.27	17	2.73	0.016	4.95	2.40	2.93
26	69	0.98	0.006	5.01	0.84	1.10	17	0.93	0.011	4.65	0.87	1.03
27	69	1.19	0.006	4.43	1.03	1.23	17	1.11	0.012	4.46	0.97	1.16
28	69	0.66	0.004	5.42	0.58	0.74	17	0.65	0.008	4.79	0.61	0.71
29	69	0.97	0.004	3.74	0.87	1.03	17	0.91	0.010	4.60	0.81	0.97
30	69	0.98	0.004	3.59	0.90	1.06	17	0.95	0.008	3.62	0.90	1.03

Fig. 14. Here too, notable exceptions to the relationship between darkness and the amount of precipitation are explained by unusually colored sands. For example, the White Sands sample was lighter than would be expected on the basis of precipitation, and the sample from near Flagstaff was darker than expected. This latter sample came from an area with a relatively high amount of precipitation, and with soils composed of black, volcanic cinders. Samples from dark, reddish sands were also darker than expected on the basis of precipitation.

With two independent color parameters, individuals of the populations can be selected to closely match the color of the substrate. The yellowish-orange pigment varies in concentration to approximate the color of the sands, which are generally some shade of tan or reddish, although both white (gypsum crystals) and black (volcanic cinders) soils occur within the range of *P. apache*. The number of black-tipped hairs seems most important in determining the overall darkness or lightness of the mice. Within limits, the actual color of the substrate appears to be less important in determining darkness, especially relative darkness, than is the amount of precipitation. Precipitation does not directly determine soil color, although it is a well-known phenomenon that soils tend to be darker colored in areas of higher precipitation, due to higher humus contents. The sandy soils upon which these mice are found have very little organic matter and essentially no surface litter, and vegetation consists mostly of small, annual forbs. The perennials that occur are generally widely scattered. The amount of vegetational cover is primarily dependent upon the amount of moisture available during the growing season of small annuals. Within the range of *P.*

Table 5.—*Continued.*

					Range						Range	
Trait	N	M	SE	CV	Minimum	Maximum	N	M	SE	CV	Minimum	Maximum
	17. *P. apache* Gran Quivira						18. *P. apache* White Sands					
1	13	130.5	1.651	4.56	120.0	139.0	51	128.7	0.677	3.76	120.0	140.0
2	13	62.4	1.010	5.83	57.0	69.0	51	62.2	0.456	5.23	56.0	68.0
3	15	68.6	0.979	5.53	63.0	74.0	54	66.2	0.448	4.98	60.0	73.0
4	15	17.6	0.114	2.56	16.7	18.1	54	18.3	0.103	4.13	16.0	20.0
5	10	6.5	0.139	6.72	6.1	7.5	48	6.5	0.072	7.67	6.0	7.5
6	13	0.898	0.020	8.10	0.783	1.063	51	0.939	0.009	6.71	0.828	1.097
7	11	22.30	0.087	1.30	21.90	22.80	52	22.47	0.073	2.35	21.35	23.80
8	12	22.28	0.087	1.36	21.85	22.75	47	22.40	0.071	2.16	21.30	23.75
9	13	5.10	0.037	2.59	4.85	5.25	54	5.17	0.023	3.30	4.50	5.45
10	15	3.14	0.062	1.98	3.00	3.25	53	3.12	0.017	4.06	2.90	3.40
11	15	4.30	0.032	2.88	4.10	4.60	54	4.21	0.015	2.67	3.85	4.45
12	15	8.05	0.085	4.10	7.35	8.50	51	8.21	0.042	3.61	7.55	8.85
13	14	12.30	0.080	2.49	11.65	12.85	48	12.40	0.042	2.39	11.65	13.00
14	14	2.73	0.050	6.84	2.35	3.05	52	2.91	0.029	7.13	2.55	3.50
15	14	4.06	0.088	8.09	3.40	4.65	52	3.94	0.035	6.40	3.15	4.35
16	13	7.94	0.057	2.57	7.60	8.25	54	8.00	0.045	4.15	7.40	8.80
17	13	2.20	0.029	4.67	2.00	2.35	53	2.21	0.018	5.78	1.90	2.55
18	14	3.83	0.038	3.71	3.60	4.00	54	3.83	0.020	3.93	3.45	4.15
19	14	4.00	0.064	5.96	3.60	4.50	51	3.76	0.035	6.64	3.10	4.15
20	14	2.80	0.017	2.32	2.70	2.85	49	2.78	0.015	3.72	2.55	3.10
21	15	0.60	0.009	5.51	0.58	0.68	48	0.56	0.007	8.59	0.48	0.68
22	15	0.64	0.009	5.57	0.61	0.79	49	0.60	0.006	7.05	0.52	0.68
23	14	0.61	0.006	3.86	0.58	0.65	49	0.62	0.005	5.72	0.55	0.71
24	14	0.72	0.007	3.61	0.68	0.77	49	0.72	0.005	5.18	0.65	0.81
25	15	2.77	0.028	3.94	2.53	3.00	49	2.67	0.009	4.83	2.40	2.93
26	15	0.97	0.011	4.54	0.90	1.03	49	0.94	0.011	8.29	0.55	1.06
27	15	1.10	0.013	4.58	1.03	1.19	49	1.06	0.006	4.36	0.97	1.23
28	15	0.65	0.008	5.02	0.58	0.71	49	0.63	0.005	5.32	0.58	0.71
29	15	0.94	0.009	3.78	0.87	1.00	49	0.92	0.006	4.43	0.87	1.00
30	15	0.97	0.012	5.19	0.87	1.06	49	0.94	0.006	4.68	0.87	1.06

apache, the growth of annuals generally occurs from June through August. Sands receiving higher amounts of moisture will have a more lush vegetational cover, and appear darker (due both to the plant cover, seen from above, and the shadows cast on the sand by vegetation). The highly significant correlation between mean annual precipitation and relative darkness is, I believe, attributable to this phenomenon, with predation being the ultimate factor determining the color of the mice.

There was no apparent geographic continuity to the observed color variation (Fig. 15), although there was a predictable pattern. Higher elevations receive more precipitation ($r = 0.60$) and have lower temperatures ($r = 0.73$), hence more moisture is available for plant growth. Samples of Apache pocket mice from higher areas such as Flagstaff, Coventry, Navajo Reservoir, Canyada Larga, San Luis Valley, Pecos, San Augustine Plains, Gran Quivira, and Casas Grandes were correspondingly dark (Table 11, Fig. 15). Color variation was very localized, and no broad pattern emerged from this analysis that would support the current arrangement of subspecies.

Color variation in *P. apache* and *P. flavescens* was similar and the same pigments appeared to be involved. *P. fasciatus* is colored differently and one can readily distinguish sympatric specimens of *P. fasciatus* and *P. flavescens* from the Great Plains by their color differences. *P. fasciatus* is darker dorsally, with an "olive" tone. The yellowish color bands of the dorsal hairs are much narrower in *P. fasciatus* and the dark-grayish basal bands show on the surface and contribute to the darker, olive tone. *P. flavescens* has a more orange lateral line. In the Uintah Basin, both *P. fasciatus* and *P. apache* have

Table 5.—*Continued.*

Trait	N	M	SE	CV	Range		N	M	SE	CV	Range	
					Minimum	Maximum					Minimum	Maximum
		19. *P. apache* Deming Plains						20. *P. flavescens copei*				
1	23	124.8	1.320	5.07	113.0	134.0	17	122.1	1.257	4.24	112.0	129.0
2	23	58.2	0.868	7.16	50.0	65.0	17	56.4	0.753	6.56	50.0	61.0
3	25	66.6	0.714	5.36	57.0	73.0	17	65.7	0.817	5.13	61.0	72.0
4	26	17.6	0.193	5.61	15.0	19.0	17	16.7	0.145	3.58	15.9	17.9
5	23	6.6	0.086	6.27	6.0	7.1	17	6.6	0.129	8.07	5.8	7.6
6	23	0.874	0.014	7.85	0.725	1.000	17	0.859	0.013	6.28	0.754	0.938
7	21	21.94	0.130	2.70	20.45	22.95	16	21.23	0.179	3.37	19.65	22.25
8	22	21.83	0.117	2.50	20.45	22.65	17	21.19	0.160	3.11	19.65	22.10
9	24	5.12	0.032	3.07	4.90	5.40	17	5.16	0.064	5.12	4.60	5.60
10	23	3.07	0.027	4.16	2.85	3.30	17	3.04	0.028	3.73	2.85	3.20
11	23	4.25	0.027	3.07	4.00	4.50	17	4.16	0.043	4.25	3.90	4.50
12	21	7.94	0.084	4.84	7.25	8.70	16	7.48	0.089	4.80	6.85	8.00
13	22	12.10	0.074	2.89	11.60	13.00	16	11.79	0.116	3.88	11.00	12.85
14	24	2.83	0.049	8.52	2.40	3.25	17	3.06	0.077	10.37	2.35	3.40
15	24	4.06	0.069	8.27	3.15	4.65	17	4.44	0.084	7.82	3.75	5.00
16	24	7.81	0.060	3.75	7.25	8.35	16	7.70	0.094	4.89	6.85	8.15
17	23	2.24	0.020	4.32	2.00	2.35	16	2.16	0.048	8.87	1.70	2.40
18	23	3.63	0.045	6.53	3.35	4.25	17	3.70	0.038	4.29	3.40	3.95
19	23	3.95	0.078	9.52	2.85	4.85	17	4.31	0.074	7.08	3.80	4.85
20	17	2.67	0.023	3.63	2.45	2.80	15	2.62	0.028	4.13	2.50	2.95
21	17	0.56	0.009	6.75	0.52	0.65	15	0.57	0.009	6.30	0.48	0.61
22	17	0.59	0.008	5.66	0.52	0.65	15	0.59	0.007	4.91	0.52	0.65
23	17	0.58	0.008	6.22	0.48	0.65	15	0.57	0.011	7.68	0.48	0.65
24	17	0.70	0.008	4.65	0.65	0.77	15	0.67	0.012	7.08	0.61	0.74
25	17	2.66	0.033	5.16	2.40	2.87	15	2.77	0.048	6.68	2.40	3.07
26	17	0.93	0.010	4.35	0.87	1.00	15	0.93	0.009	3.88	0.84	0.97
27	17	1.07	0.009	3.52	1.00	1.13	15	1.04	0.011	4.01	0.97	1.13
28	17	0.64	0.010	6.26	0.58	0.71	15	0.62	0.012	7.61	0.55	0.68
29	17	0.94	0.009	4.21	0.84	1.00	15	0.87	0.015	6.62	0.81	0.97
30	17	0.95	0.011	5.09	0.84	1.03	15	0.90	0.012	5.05	0.81	0.97

about the same degree of relative darkness, but *P. apache* has a pale yellowish-orange (Light Ochraceous-Buff) color, and *P. fasciatus* has a pale olive-yellow color (near Cream-Buff or Chamois). I have found these color differences to be reliable for distinguishing these taxa.

Multivariate Analyses

The matrix of taxonomic distances is presented in Table 12. The least similar samples have the largest distance coefficients. These data are summarized in the phenogram of Fig. 16. Note four main clusters, a *P. fasciatus* cluster (samples 1–4), a *P. apache* cluster encompassing the southern and western samples (samples 7 through 13, in descending order in Fig. 16), a *P. apache* cluster of northern samples (samples 5, 6, 10, and 12), and a *P. flavescens* cluster (samples 20 and 21). Two principal deficiencies in the phenogram are apparent. All samples had an equal chance of being linked regardless of their geographic positions, and in clustering samples, many of the intersample relationships were simply lost. The coefficient of cophenetic correlation (derived from a distance-cophenetic matrix comparison) is a measure of the amount of information lost in the phenogram. This value (0.77) falls near the lower end of the range reported by Sneath and Sokal (1973). The phenogram is weakest in adequately portraying relationships at the more distant levels. Placing the distance values in their geographic context (Fig. 17) corrects some of these deficiencies and alters the interpretations derived from the phenogram. The sample of *P. f. copei* was about equally similar to the Deming Plains sample and to *P. f. flavescens*. Samples of Apache and olive-backed pocket mice from the Uintah Basin were

Table 5.—*Continued.*

Trait	N	M	SE	CV	Range	
					Minimum	Maximum
			21. *P. f. flavescens*			
1	10	121.7	1.453	3.78	114.0	128.0
2	10	58.7	1.350	7.27	52.0	65.0
3	11	62.7	0.702	3.71	60.0	66.0
4	11	16.8	0.122	2.41	16.0	17.0
5	11	6.5	0.157	7.98	6.0	7.0
6	10	0.931	0.026	8.23	0.839	1.083
7	8	21.39	0.120	1.59	20.90	21.85
8	8	21.39	0.120	1.59	20.90	21.85
9	9	4.99	0.042	2.52	4.85	5.20
10	10	3.02	0.038	3.99	2.85	3.25
11	9	4.21	0.034	2.41	4.10	4.40
12	9	6.98	0.095	4.07	6.45	7.35
13	9	11.46	0.102	2.76	10.95	11.90
14	9	3.01	0.044	4.43	2.90	3.35
15	9	5.01	0.074	4.42	4.75	5.40
16	9	7.53	0.078	3.11	7.10	7.80
17	8	2.22	0.028	3.60	2.10	2.30
18	9	3.72	0.034	2.78	3.60	3.90
19	8	4.92	0.117	6.71	4.15	5.20
20	5	2.64	0.024	2.07	2.60	2.70
21	6	0.52	0.013	6.08	0.48	0.58
22	6	0.60	0.014	5.67	0.55	0.65
23	6	0.57	0.013	5.51	0.55	0.61
24	6	0.67	0.018	6.61	0.61	0.74
25	6	2.74	0.020	1.82	2.67	2.80
26	6	0.92	0.023	6.11	0.87	1.03
27	6	1.04	0.018	4.22	1.00	1.10
28	5	0.63	0.030	10.58	0.55	0.71
29	6	0.85	0.007	1.96	0.84	0.87
30	6	0.90	0.019	5.29	0.84	0.97

distant phenetically, as were samples of the olive-backed and plains pocket mice. The relatively small distances linking neighboring samples 5, 6, 10, 12, 15, and 17 reinforce the previous interpretation that these samples represent a more or less continuous population. Peripheral populations in Arizona (7 and 8), the San Luis Valley (13), and the San Augustine Plains (16) showed high similarity to only one or two other samples (see Table 12 for coefficients of distance not depicted in Fig. 17). The Gran Quivira sample (17) was about equally distant to the Rio Grande Valley (15) and White Sands (18) samples. Gene exchange between the White Sands and Gran Quivira populations is not too likely today, but this route may have only recently been blocked. Large lava flows, of fairly recent age, and upland rocky terrain constrict the Tularosa Valley north of the White Sands, and any movement along this route would be through non-sand habitats.

A matrix of similarity, based upon the Q-mode correlation analysis, is given in Table 13, summarized in the phenogram of Fig. 18, and the data placed in a geographic context in Fig. 19. The higher the similarity values, the greater the similarity between samples. Note in the phenogram (Fig. 18) a *P. fasciatus* cluster (samples 1–4), a cluster including *P. flavescens* and a set of neighboring samples of Apache pocket mice (samples 9, 16, 19, 20, and 21), and a *P. apache* cluster. Those closely linked samples (that is, 1 and 2, 3 and 4, 5 and 6, 7 and 8, 10 and 12, and 20 and 21) are ones that are geographic neighbors and were shown to be closely similar in the other analyses. Otherwise, these two phenograms do not appear to be too similar (Figs. 16 and 18). A matrix comparison between the matrices of distance and similarity showed only an approximate 50% ($r = -0.51$) correspondence. They differed most in the linkages of the more dissimilar

Table 6.—*Interpopulation matrix of correlation between morphometric traits. The numbers of the traits correspond to those in Table 1. Degrees of freedom = 19.*

Traits	1	2	3	4	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1	—																											
2	.85	—																										
3	.84	.68	—																									
4	.56	.71	.25	—																								
6	.44	.70	–.10	.63	—																							
7	.89	.69	.76	.61	.37	—																						
8	.90	.72	.78	.59	.35	.99	—																					
9	.40	.42	.15	.67	.48	.54	.52	—																				
10	.80	.71	.66	.69	.38	.81	.80	.37	—																			
11	.78	.56	.71	.35	.30	.86	.85	.24	.72	—																		
12	.69	.57	.55	.61	.37	.86	.84	.61	.66	.74	—																	
13	.72	.59	.56	.64	.39	.89	.86	.64	.73	.74	.97	—																
14	–.06	–.09	–.19	.26	.20	.23	.20	.49	.24	.24	.27	.34	—															
15	–.17	–.34	.02	–.69	–.36	–.16	–.14	–.51	–.28	.11	–.36	–.34	–.02	—														
16	.83	.55	.81	.40	.17	.93	.93	.36	.78	.87	.77	.78	.21	.06	—													
17	.51	.56	.36	.65	.32	.59	.57	.50	.66	.35	.47	.56	.21	–.22	.50	—												
18	.32	.24	.20	.26	.21	.43	.45	.41	.35	.15	.26	.32	.33	–.06	.39	.27	—											
19	–.22	–.33	.00	–.70	–.41	–.35	–.32	–.68	–.35	–.07	–.58	–.55	–.30	.91	–.16	–.26	–.23	—										
20	.84	.77	.63	.67	.51	.89	.88	.46	.92	.80	.76	.79	.31	–.24	.83	.53	.45	–.40	—									
21	.81	.56	.83	.25	.12	.74	.74	.13	.73	.82	.64	.64	–.05	.08	.85	.30	.15	–.01	.74	—								
22	.72	.49	.77	.05	.06	.64	.65	–.12	.63	.79	.47	.47	–.16	.32	.78	.23	.11	.26	.65	.91	—							
23	.76	.69	.58	.62	.44	.81	.81	.39	.76	.69	.68	.67	.23	–.33	.71	.42	.37	–.43	.88	.59	.50	—						
24	.81	.71	.66	.52	.42	.78	.77	.22	.85	.74	.64	.64	.01	–.29	.76	.32	.28	–.36	.88	.77	.70	.82	—					
25	.61	.57	.46	.46	.31	.67	.65	.52	.62	.58	.56	.61	.32	.04	.65	.65	.23	–.15	.65	.50	.43	.47	.37	—				
26	.63	.47	.56	.30	.23	.73	.70	.08	.79	.84	.62	.64	.25	.10	.82	.42	.22	–.09	.79	.79	.79	.64	.73	.57	—			
27	.63	.48	.50	.49	.35	.78	.76	.34	.81	.85	.67	.70	.49	–.11	.79	.38	.35	–.33	.86	.68	.56	.74	.76	.55	.87	—		
28	.68	.42	.72	.09	.07	.68	.68	–.05	.57	.84	.53	.49	–.07	.33	.79	.20	–.04	.22	.63	.85	.91	.57	.67	.46	.77	.60	—	
29	.47	.55	.22	.79	.50	.55	.53	.67	.69	.35	.56	.61	.40	–.73	.38	.56	.35	–.79	.68	.26	.02	.64	.58	.35	.34	.62	.00	—
30	.76	.60	.67	.52	.30	.80	.79	.25	.86	.79	.63	.64	.21	–.23	.78	.37	.38	–.34	.91	.75	.64	.85	.90	.43	.78	.89	.64	.66

Table 7.—*Factor scores for the first five factors extracted from a matrix of correlation.*

Sample	Factors				
	I	II	III	IV	V
1. *Perognathus fasciatus fasciatus*	–0.26180	2.47176	–0.78360	1.84415	–1.12312
2. *Perognathus fasciatus olivaceogriseus*	–0.48409	2.26763	–0.08344	0.27492	0.59393
3. *Perognathus fasciatus litus*	0.80838	1.51588	–0.74339	2.45487	–0.47299
4. *Perognathus fasciatus callistus*	0.62812	1.01588	–0.12778	1.29386	0.14666
5. *Perognathus apache* Uintah Basin	1.59702	0.57906	2.17739	–1.32724	–2.18045
6. *Perognathus apache* Moab	1.49471	–0.40347	1.05894	1.69595	2.39596
7. *Perognathus apache* Painted Desert	–0.07471	–0.66931	0.14526	0.58163	–0.56386
8. *Perognathus apache* Flagstaff	–0.34763	–0.78385	0.17254	0.83553	–1.47170
9. *Perognathus apache* Gallup	0.22867	0.16594	1.83041	–1.58717	–1.32679
10. *Perognathus apache* San Juan Basin	1.67000	–1.20200	–0.83880	1.01375	2.61925
11. *Perognathus apache* Canyon Largo	0.18009	–0.16779	–0.23676	–1.55194	–0.52558
12. *Perognathus apache* Estrella	0.84708	–0.03241	1.18789	–1.13915	–1.20545
13. *Perognathus apache* San Luis Valley	–0.56873	–1.38406	–1.44469	2.01622	–0.42079
14. *Perognathus apache* Santa Fe	0.44337	–0.62562	–1.69960	0.36607	1.25001
15. *Perognathus apache* Rio Grande Valley	0.34882	0.06618	0.81357	–0.12503	–0.64501
16. *Perognathus apache* San Agustine Plains	–0.64491	–0.50534	–0.73553	1.38297	0.32324
17. *Perognathus apache* Gran Quivira	–0.44968	–0.03960	–1.05570	–1.90546	–1.56102
18. *Perognathus apache* White Sands	–0.56426	–1.18087	0.05141	–0.42458	–0.13820
19. *Perognathus apache* Deming Plains	1.15288	0.61484	0.05253	1.77366	1.43557
20. *Perognathus flavescens copei*	–1.94565	–0.30397	1.28590	0.31711	–0.02803
21. *Perognathus flavescens flavescens*	–2.25961	0.70574	1.81326	0.86707	2.04352
Cumulative % of total variance	56.1	71.7	77.4	81.6	85.1

samples. The shortcomings noted for the distance phenogram are also apparent in the similarity phenogram. Namely, much information was lost (the coefficient of cophenetic correlation is 0.73), and the geographic relationships were obscured. The same overall pattern of intersample relationships are apparent in the similarity map of Fig. 19 as was shown in the distance map (Fig. 17). Samples 5, 6, 10, 12, 15, and 17 form a geographic chain, with sample 15 being the weakest link between the more northern and more southern populations. Peripheral populations exhibited much the same relationships to other samples as were shown on the distance map. Some differences stand out, such as the Canyon Largo sample (11), which was most similar to the San Juan Basin sample (10), and was particularly dissimilar to the Santa Fe sample (14). The Painted Desert sample (7) showed little similarity to the San Augustine Plains sample (16), and was more similar to the San Juan Basin sample in this analysis than in previous ones. The Deming Plains sample (19) was most similar to *P. f. copei* (20), but *copei* was much closer to *P. f. flavescens* (21) than to the Deming Plains sample.

The differences in computational procedures account for much of the disparity between these distance and similarity analyses. Taxonomic distance is a measure of the Euclidean distance separating the samples arrayed, in this case, in 29 dimensional hyperspace. The closer two samples are, the more similar they will be in both size and proportions of all 29 characters. Q-mode correlation analysis, on the other hand, measures the correspondence between the columns (samples) in a matrix of 29 rows. If two samples differ in size, but have the same body proportions, they would have a similarity value of 1.0. Samples could be significantly different in the size of all traits and have relatively large distance values, yet exhibit similar proportions and have high similarity values. Conversely, samples with no significant differences in size (for example, samples 11 and 14), but which differ proportionately ($Q - r = 0.07$), appear to be quite close phenetically ($d = 0.59$). Samples that are shown to be quite similar by both procedures are probably closely related.

A principal components analysis of the matrix of correlation yielded results very similar to the other factor analysis, and reinforced the conclusions of the other multivariate analyses. The first five principal components accounted for 89.6% of the total variance. The scores for the first three principal

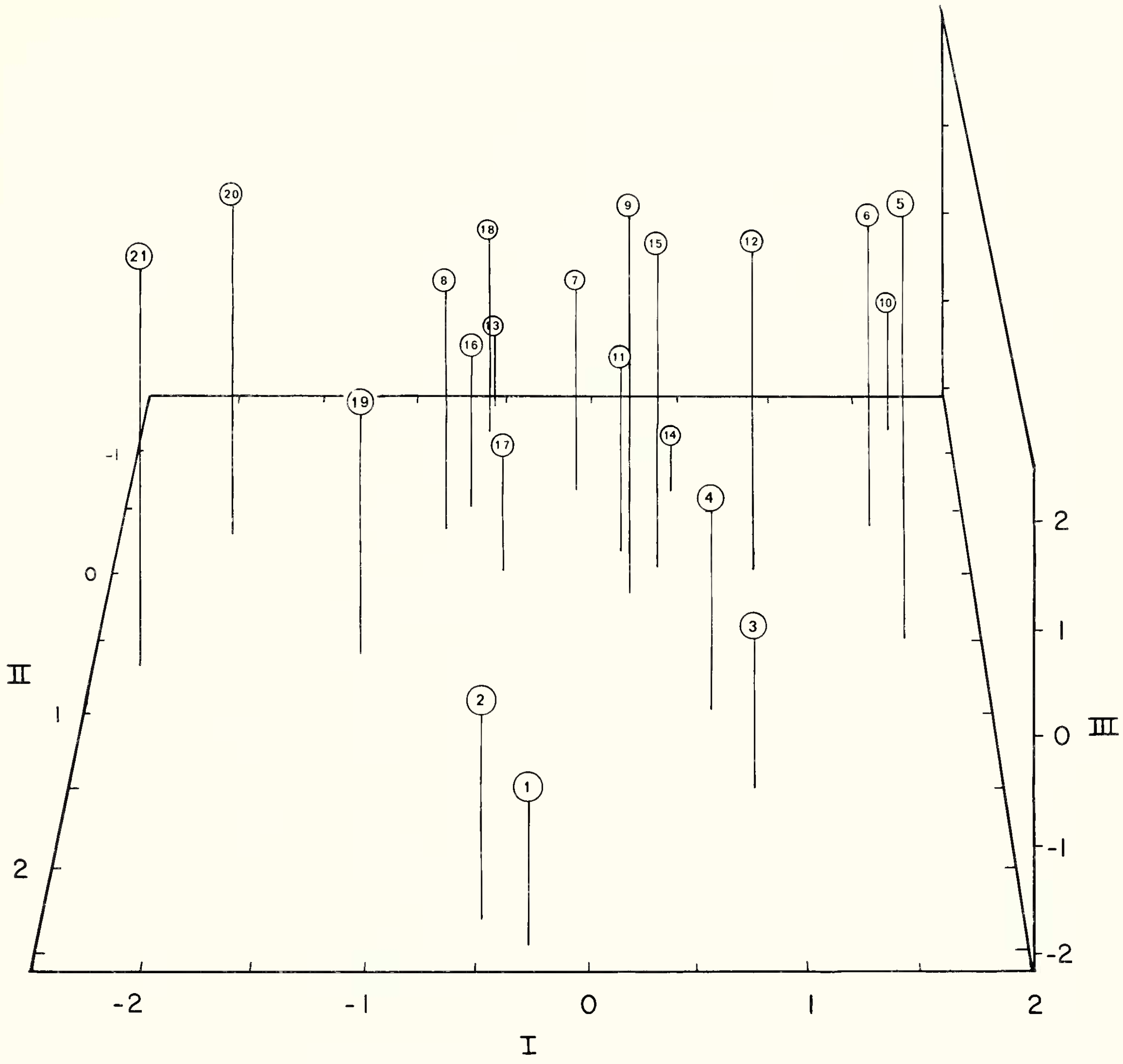

Fig. 8.—Three-dimensional plot of first three factors, extracted from the matrix of correlation, for samples of the *Perognathus fasciatus* species group. The sample codes are defined in the text and Table 7, and are shown in Fig. 4.

components for each of the samples are plotted in Fig. 20. Component I accounted for 58.3% of the total variance, and is the size component. Only width of interparietals and least interbullar distance were loaded negatively on component I. Component II, accounting for 16.8% of the variance, exhibited highest negative loading on traits expressing the constriction of the postcranial region (IPW, LID) and the width of P_4. Traits with high positive loading were length of hind foot, skull length (ONL) and length of M_1. Component III was most highly loaded by traits measuring external dimensions (TOTL, TL, HBL with positive coefficients), and bullar inflation (BW with a negative coefficient). Note, by comparing Figs. 8 and 20, that the principal components and factor analyses yielded similar results, except that the images are rotated on the horizontal axis. There are other minor differences

Table 8.—*Summary of SS-STP analysis between geographically adjacent samples. Refer to Table 7, the text, or Figs. 4 or 9 for an explanation of sample codes. + = significant difference; − = nonsignificant difference.*

	Traits																														
Samples	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Total
1–2	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	0
1–21	+	−	+	−	+	−	+	+	−	+	+	−	−	+	−	+	−	−	−	−	+	+	−	+	−	−	−	+	−	+	14
2–3	+	+	−	−	−	−	+	+	−	+	−	+	+	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	8
2–4	−	−	−	−	−	−	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	2
2–20	+	+	+	−	+	−	−	−	−	−	−	−	−	+	−	+	−	−	−	−	−	+	−	−	−	+	−	+	−	−	9
2–21	+	−	+	−	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	+	+	−	−	−	+	−	+	−	−	8
3–4	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	0
3–5	−	−	−	−	−	−	−	−	+	−	−	−	−	+	−	−	−	−	+	+	−	−	−	−	−	−	+	−	+	+	7
4–5	−	−	−	−	−	−	+	+	−	−	−	−	−	+	−	−	−	+	+	+	−	−	−	−	−	−	+	−	+	+	9
5–6	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	1
6–7	−	−	−	−	−	−	+	+	−	−	−	−	−	+	+	+	−	−	−	+	−	−	−	−	−	−	+	−	+	−	8
6–10	−	−	−	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	2
6–11	−	−	−	−	−	−	+	+	−	−	+	+	+	+	+	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	9
7–8	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	1
7–9	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	1
7–10	−	−	−	+	−	−	+	+	−	+	−	−	−	−	−	+	−	+	−	+	+	−	+	−	−	+	+	+	+	+	14
8–9	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	1
8–16	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	2
9–10	−	+	−	+	−	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	5
9–12	−	+	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	2
9–15	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	1
9–16	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	+	−	−	−	−	−	+	−	−	+	−	4
10–11	−	−	−	+	−	−	+	+	−	−	−	+	+	+	−	−	+	+	−	+	−	−	−	−	−	−	−	−	−	−	9
10–12	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	1
11–12	−	−	−	+	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	2
11–14	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	0
12–14	−	−	−	+	−	−	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	4
12–15	−	+	−	−	−	+	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	3
13–14	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	+	−	−	−	4
14–15	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	0
14–17	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	0
14–20	+	+	+	+	−	−	+	+	−	+	+	−	−	−	+	−	−	−	−	+	−	+	−	+	−	+	+	−	+	+	16
15–16	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	1
15–17	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	2
15–18	−	−	+	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	+	+	−	−	−	−	+	−	+	−	6
15–19	+	+	−	+	−	−	+	+	−	+	−	−	−	−	−	+	−	−	−	+	−	+	−	−	−	−	−	−	−	−	9
16–19	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	0
17–18	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	1
17–19	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	−	−	−	−	−	−	−	−	2
17–20	+	−	−	−	−	−	−	+	−	−	−	+	−	−	+	−	−	−	−	+	−	−	−	−	−	+	−	−	+	−	7
18–19	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	1
18–20	−	+	−	+	−	+	+	+	−	−	−	+	+	−	+	−	−	−	+	+	−	−	+	−	−	−	−	−	+	−	12
19–20	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	2
20–21	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	1

(the factor analysis was based upon the unstandardized data of a 30 characters matrix, whereas the principal components analysis utilized standardized data in a 29 characters matrix), but the differences seem relatively trivial. Note in Fig. 20 that the Apache and plains pocket mice samples differed mostly in size (Component I). The olive-backed pocket mice differed from the others in having small bullae, short skulls, unconstricted crania, small feet, large lower premolars, and short lower first molars. The San Luis Valley sample was the most distinctive of the Apache pocket mice, having short tails and wide crania (Component III), but paralleled the White Sands sample in Components I and II.

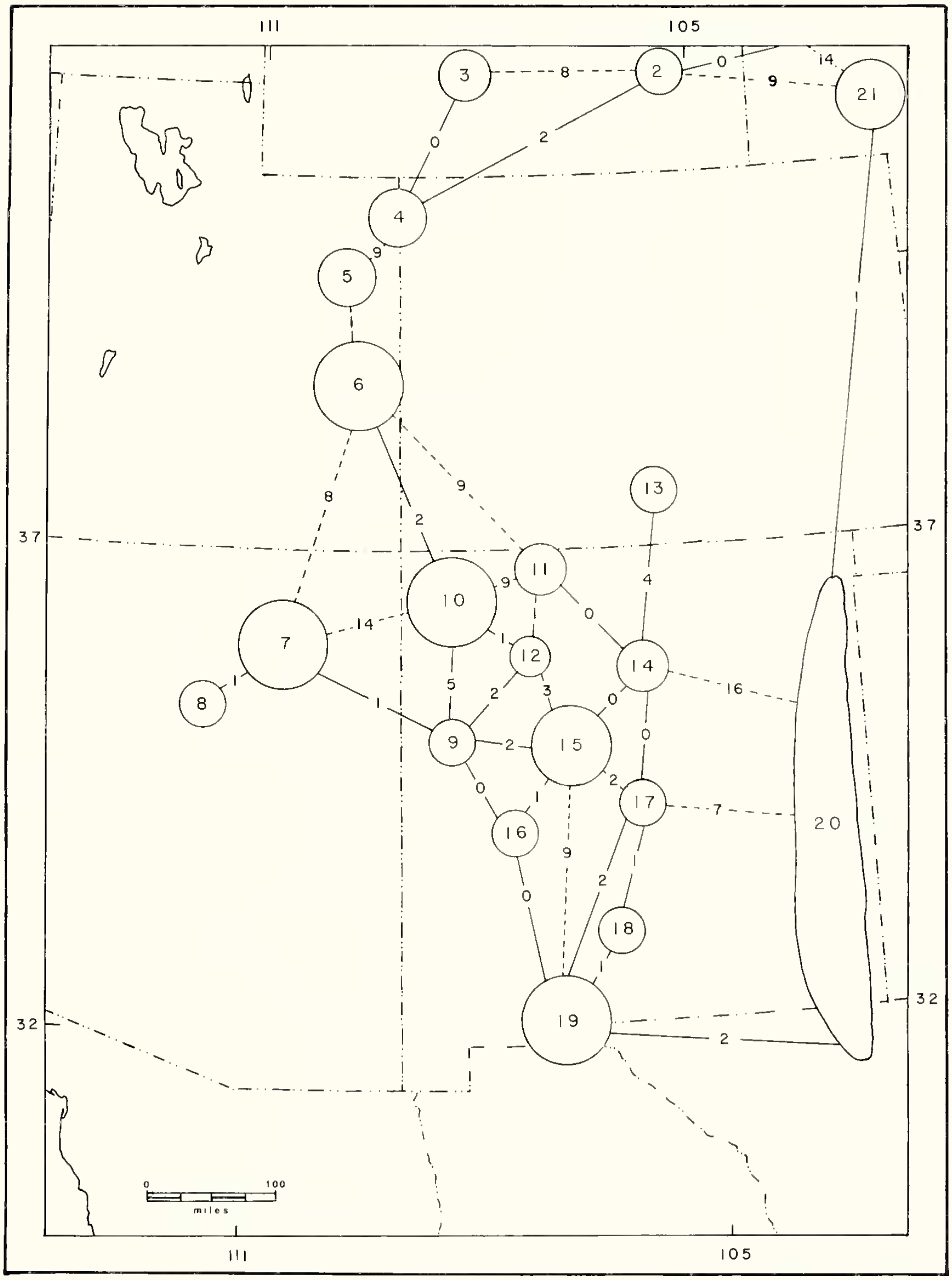

Fig. 9.—Map depicting the number of significant differences between adjacent samples of the *Perognathus fasciatus* species group, based upon the SS-STP analysis. The lines extending northward from samples 2 and 21 represent intersample comparisons with sample 1 (*P. f. fasciatus* from parts of North and South Dakota). The geographic positions of the samples are only approximations. Solid lines represent most likely routes of gene exehanges, and broken lines represent unlikely routes of gene exchange, based upon the number of significant differences between samples.

The lines in Fig. 20 connect samples sharing the same centroid. Seven centroids extracted from the distance matrix and the distances of each sample to its closest centroid are shown in Fig. 21. This summary technique resulted in a much more satisfactory geographic grouping of samples than was the case with the phenograms. Only one sample (13) was erroneously placed with a nonneighboring sample. The San Luis Valley sample was closest to the Painted Desert sample, as shown in the centroid

Table 9.—*Coefficients of correlation between morphometric traits, color indices, and climatic and geographic variables for samples of* P. apache. *DI = darkness; RI = richness; RDI = relative darkness; AEL = elevation adjusted for latitude; CS = climatic severity index; EL = elevation; GS = growing season; Lat = latitude; MJT = mean July minimum temperature; MP = mean annual precipitation; MT = mean annual temperature. Refer to Table 1 for a list of traits. The degrees of freedom for the morphometric traits and the color indices are 14 and 33, respectively.*

Trait	CS	LAT	EL	GS	MT	MP	MJT	AEL
1	.40	.84**	.18	−.34	−.54*	−.31	−.42	−.01
2	.34	.65**	.21	−.25	−.39	−.29	−.26	−.13
3	.36	.68**	.27	−.33	−.53*	−.11	−.44	.16
4	.35	.39	.17	−.29	−.36	−.29	−.27	.01
6	.19	.60**	−.04	−.12	−.25	−.40	−.14	−.20
7	.19	.75**	−.12	−.19	−.31	−.40	−.28	.18
8	.21	.75**	−.10	−.21	−.34	−.39	−.30	.14
9	.26	.60**	−.19	−.21	−.34	−.50*	−.26	−.47
10	.29	.61**	.06	−.33	−.30	−.15	−.23	.38
11	−.07	.78**	−.23	.08	−.17	−.27	−.11	.39
12	−.08	.58*	−.37	.07	−.04	−.58*	−.07	.20
13	.07	.66**	−.23	−.09	−.19	−.50*	−.20	.26
14	−.26	.33	−.58*	.14	.15	−.26	.13	.33
15	−.31	.17	−.47	.22	.19	−.09	.20	.29
16	.09	.69**	−.25	−.15	−.22	−.26	−.18	.36
17	.21	.29	.04	−.18	−.16	−.13	−.07	.04
18	.15	.28	−.12	−.28	−.19	−.37	−.18	−.02
19	−.04	−.12	.16	.03	−.06	.29	.04	−.01
20	.21	.72**	−.08	−.22	−.27	−.32	−.22	.27
21	.16	.72**	−.02	−.18	−.34	−.10	−.24	.39
22	.10	.67**	.00	−.14	−.25	−.07	−.17	.48
23	.23	.69**	−.06	−.26	−.29	−.20	−.30	.12
24	.18	.63**	−.04	−.21	−.22	−.16	−.18	.30
25	.25	.63**	−.08	−.22	−.23	−.17	−.17	.13
26	−.05	.56*	−.25	−.02	−.01	−.07	.01	.67**
27	−.03	.69**	−.26	−.02	−.12	−.17	−.08	.54*
28	.12	.77**	−.17	−.14	−.25	−.14	−.23	.39
29	.21	.60**	.05	−.15	−.27	−.13	−.20	.08
30	.11	.67**	−.08	−.12	−.20	−.21	−.16	.37
DI	—	.13	.28	—	−.36*	.50**	—	.31
R1	—	−.14	.45**	—	−.23	.64**	—	.30
RD1	—	−.04	.43**	—	−.31	.66**	—	.34

* $P \leq 0.05$; ** $P \leq 0.01$.

analysis, but was next most distant to the Santa Fe sample (Table 12, or Fig. 17), with which it has its only geographic affinities.

Discriminant function and canonical analysis provided a technique whereby individuals of each sample could be tested for phenetic fidelity to their populations, and the distances between individuals could be measured. As only individuals with complete data could be utilized, length of ear was excluded, and some of the smaller samples were either submitted for classification only or were combined with other samples. Table 14 is a classification matrix, based upon the squared Mahalanobius distance of individuals from the nearest group means on the discriminant functions. The samples listed in the columns of Table 14 were those utilized in computing the discriminant functions and F statistics. Samples in the rows without a corresponding column were submitted for classification only. Note that only one *P. fasciatus* was misclassified as a *P. flavescens*, and that only three Apache pocket mice were closest to *P. fasciatus*. Three Apache pocket mice were placed with the plains pocket mice, and two plains pocket mice were classified as Apache pocket mice. Overall, the individuals showed relatively high group fidelity, and misclassifications were most between neighboring groups. Samples showing relatively little misclassification were the San Luis Valley, the Uintah Basin, Moab, and the *P. fasciatus* samples.

Table 10.—*Coefficients of correlation between climatic and geographic variables. The abbreviations are defined in Table 9. Degrees of freedom = 14.*

	CS	LAT	EL	GS	MT	MP	MJT	AEL
CS	—							
LAT	.33	—						
EL	.75**	.01	—					
GS	–.96**	–.28	–.65**	—				
MT	–.89**	–.52*	–.74**	.83**	—			
MP	.21	–.23	.46	–.24	–.22	—		
MJT	–.90**	–.42	–.72**	.87**	.96**	–.26	—	
AEL	–.25	–.07	–.10	.14	.23	.35	.17	—

* $P \leq 0.05$; ** $P \leq 0.01$.

Table 15 lists the group means of the first five canonical variables and their cumulative proportions of the total dispersion. Twelve canonical variables accounted for 100% of the dispersion, although variables beyond the third individually accounted for relatively little. The sample means of the first two canonical variables are plotted in Fig. 22. The encircled areas correspond to the distribution of the 457 individual cases. There was considerable overlap within the samples of *P. fasciatus*, *P. apache*, and *P. flavescens*, and between samples of *P. apache* and *P. flavescens*, but essentially none between *P. fasciatus* and the other taxa. A single specimen of *P. apache* from the Moab sample overlapped the position of the *P. fasciatus* sample (Fig. 22). The overlap between *P. apache* and *P. flavescens* included numerous specimens from several samples of both taxa. Note that the uppermost sample of *P. apache* (5) is from the Uintah Basin, and that the spatial relationships of the *P. apache* samples in Fig. 22 are nearly the same as their geographic relationships (see, for example, Fig. 21). The *P. fasciatus* samples, starting on the right side of Fig. 22, are distributed from northeast to southwest. Starting on the lower left side of the *P. flavescens* samples, individuals are distributed from southwest to northeast. With only a little distortion, Fig. 22 could be placed over a map, and the geographic positions of the samples would nearly correspond to their positions on canonical variates I and II. The space in the middle of the samples would fit over the Rocky Mountains in Colorado and New Mexico.

CONCLUSIONS

In summarizing the patterns of structural variation, it must be emphasized that the latitudinal size cline in the Apache pocket mouse populations is the dominant trend. Apache pocket mice are larger in colder and more northern areas. With increasing size the posterior cranial region becomes progressively more constricted and the length of the tail increases at a rate faster than the length of the head and body. Imposed upon the general size cline are significant relationships between relative amounts of moisture and bullar and rostral sizes. Generally, these skull parts increase with increasing body size, but the rates of increase are apparently also influenced by the amount of available moisture. Small mice from drier areas have as large or larger bullae than larger mice from moister sites. Rostral size increases at a slower rate with increasing moisture. Color is strongly associated with a combination of climatic and local edaphic soil factors that together determine relative substrate darkness. In general, mice from higher, moister elevations or latitudes are darker than those from lower, drier climes. This relationship is modified by unusually light or dark colored sands.

Apache pocket mice are primarily limited to loose sands and this habitat type is relatively uncommon and discontinuously distributed. Therefore, most populations are probably small and well isolated from their neighbors. Under such circumstances, populations can quickly evolve according to the dictates of local selective forces. This undoubtedly explains the great amount of local variation in color, and the relatively great degree of morphometric variation over short distances. Several peripheral populations have apparently evolved along parallel paths, due to similar selective forces. Most of these

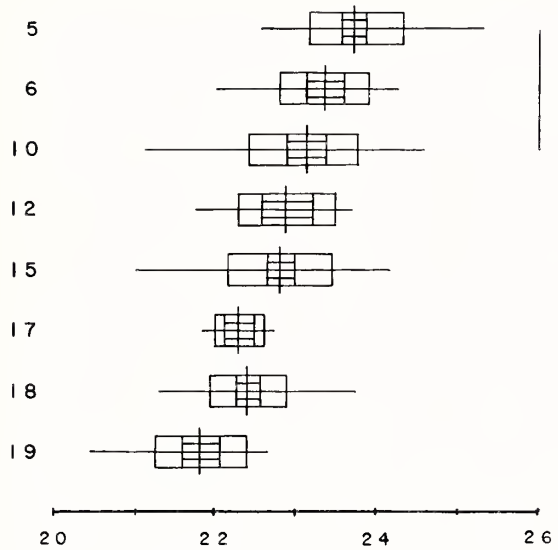

Fig. 10.—North-south variation in occipitonasal length for adjacent samples of *Perognathus apache*. Samples are arranged from north to south. Vertically arrayed numbers are sample codes (see Fig. 9). The scale is in mm. Horizontal lines depict the sample ranges; the vertical lines mark the sample means; the outer rectangles encompass ±1 SD from the mean; the inner rectangles encompass ±2 SE from the mean; and the vertical lines on the right side of the diagram connect nonsignificant subsets, based upon the SS-STP analysis.

populations live in higher, moister areas, although there are some parallel developments in populations from drier sites too.

Plains pocket mice, in contrast, are less variable over much greater distances. The same trends in variation are apparent, but are not nearly so dramatic. Plains pocket mice from the drier southern and western portions of their geographic range have larger bullae and slightly more constricted crania and larger rostra than the more mesic-adapted northern and eastern populations. The relatively uniform topography and the gradually changing climatic patterns of the Great Plains have resulted in selection for a more uniform and gradually varying population.

Populations of the olive-backed pocket mouse exhibit a similar pattern of geographic variation in relationship to changing climatic patterns. Some structural convergence with *P. apache* can be seen in populations that approach the range of the Apache pocket mouse (see Fig. 20). A size cline in the *P. fasciatus* samples runs from northeast (small mice) to southwest (larger mice). This does not defy Bergman's principle, as elevational increases and corresponding temperature decreases occur from northeast to southwest. Along the same transect, aridity increases from northeast to southwest, and there is a corresponding increase in the relative bullar and rostral sizes, and color becomes progressively lighter.

Table 11.—*Mean values for color indices of samples of* Perognathus apache *and* P. flavescens. *Sample numbers are as defined in the text and shown in Fig. 4. Within samples, localities are arranged from north to south, as shown in Fig. 15. DI = darkness; RI = richness; RDI = relative darkness (darkness + richness).*

Locality	Sample	DI	RI	RDI
Uintah Basin, UT	5	3.9	2.1	6.0
Fruita-Rifle, CO	6	4.7	2.2	6.8
Green River (city), UT	6	3.8	1.2	5.0
Dewey-Castle Valley, UT	6	4.0	4.7	8.7
Moab, UT	6	4.4	4.5	8.9
Coventry, CO	–	4.0	5.0	9.0
Navajo Mtn, UT-Page, AZ	–	3.8	4.3	8.2
Tuba City, AZ	7	3.2	3.4	6.6
Oraibi, AZ	7	2.5	2.6	5.1
Keam's Canyon, AZ	7	2.9	3.4	6.3
Zuni Well, AZ	7	4.0	4.0	8.0
Holbrook-Winslow, AZ	7	2.4	2.8	5.2
Flagstaff-Winona, AZ	8	4.7	5.0	9.7
Gallup, NM	9	3.7	4.0	7.7
El Morro, NM	9	3.0	5.0	8.0
Chaco Wash, NM	10	2.5	2.3	4.8
Navajo Reservoir, CO, NM	11	4.7	5.0	9.7
Canyon Largo, NM	11	3.0	2.5	5.5
Canyada Larga, NM	11	4.3	4.3	8.6
Estrella, NM	12	3.2	3.0	6.2
San Luis Valley, CO	13	4.7	3.8	8.5
Espanola, NM	14	3.4	3.0	6.5
Santa Fe, NM	14	4.1	3.9	8.0
Pecos, NM	14	4.7	4.1	8.8
Albuquerque, NM	15	3.0	2.5	5.5
Socorro, NM	15	3.1	3.3	6.5
San Augustine Plains, NM	16	4.8	4.0	8.8
Gran Quivira, NM	17	4.3	4.2	8.5
White Sands, NM	18	2.6	0.2	2.8
Engle, NM	19	4.3	3.6	7.9
Las Cruces, NM	19	4.0	3.4	7.4
El Paso, TX	19	4.0	4.0	8.0
Samalayucca, CH	19	2.7	2.3	5.0
Casas Grandes, CH	19	4.1	4.5	8.6
Willcox, AZ	—	3.0	3.2	6.2
Clayton, NM	20	2.0	3.0	5.0
Logan, NM	20	3.7	3.8	7.5
Tolar, NM	20	3.9	4.6	8.5
Caprock (Mescalero Sands), NM	20	4.0	4.5	8.5
Jal-Carlsbad, NM	20	3.3	3.2	6.5
Mentone, TX	20	3.0	4.0	7.0

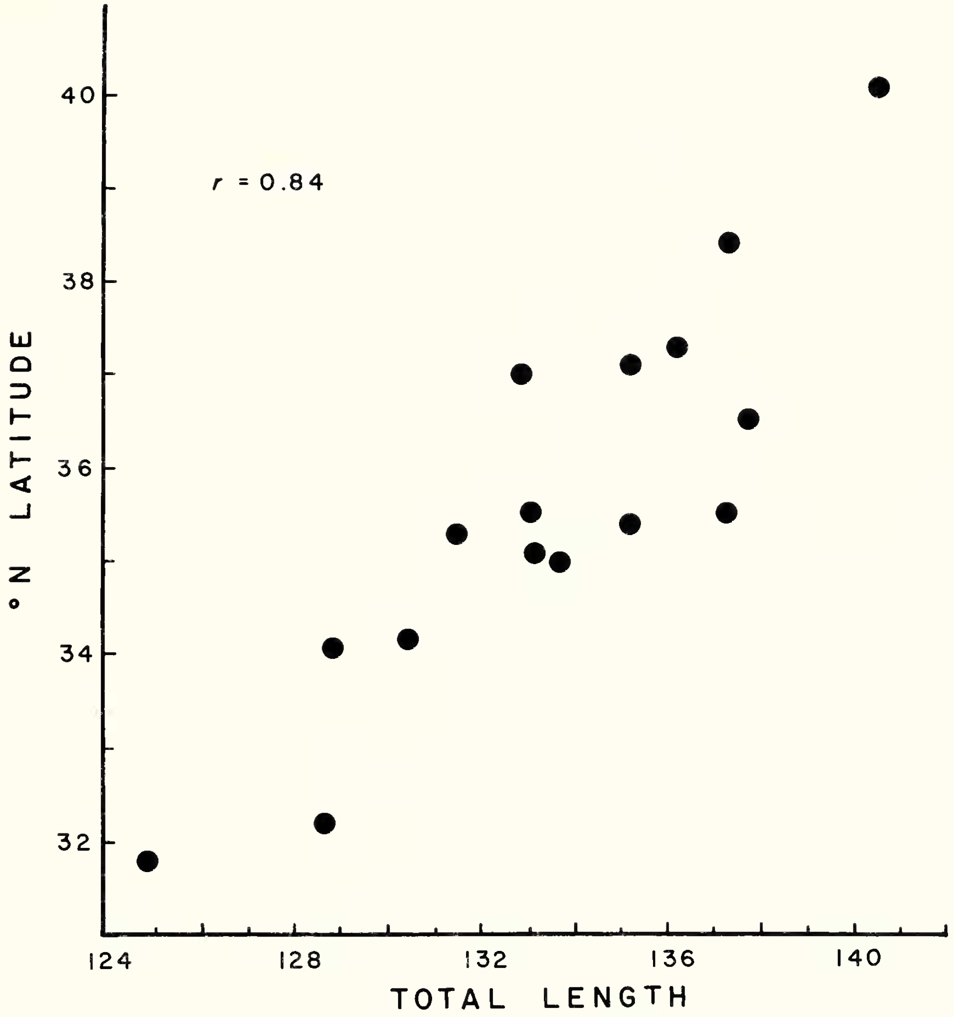

Fig. 11.—Two dimensional plot, depicting geographic variation in total length (in mm) of samples of *Perognathus apache*, $P < 0.001$.

Speciation

Only two major taxonomic units are apparent from the data presented in this study. One unit, *P. fasciatus*, is the more northern and shows adaptations for life in a cooler, moister environment. It is relatively dark colored and large bodied, with a short tail, small bullae, narrow interorbital region, and an unconstricted cranium. The more southern unit, represented by Apache and plains pocket mice, exhibits adaptations for life in a warmer and drier climate. The Great Plains populations are lighter colored and smaller bodied, with relatively larger bullae than *P. fasciatus*. The intermountain plateau populations are much more variable, as should be expected from the great amount of topographic and climatic variability within their range. The variability of the mice follows a predictable course, with temperature and moisture factors, and, perhaps, competition from congeners determining to a great degree the size and shape of individuals in each population.

I envision that these two units arose from a parent population which was widely distributed in the Great Plains and intermountain plateaus. Adaptation to local environmental conditions was probably similar to that exhibited by extant populations. The events leading to speciation may have been initiated as late as the last interglacial period (Sangamon), although speciation at an earlier time seems equally feasible. At the close of of the interglacial period,

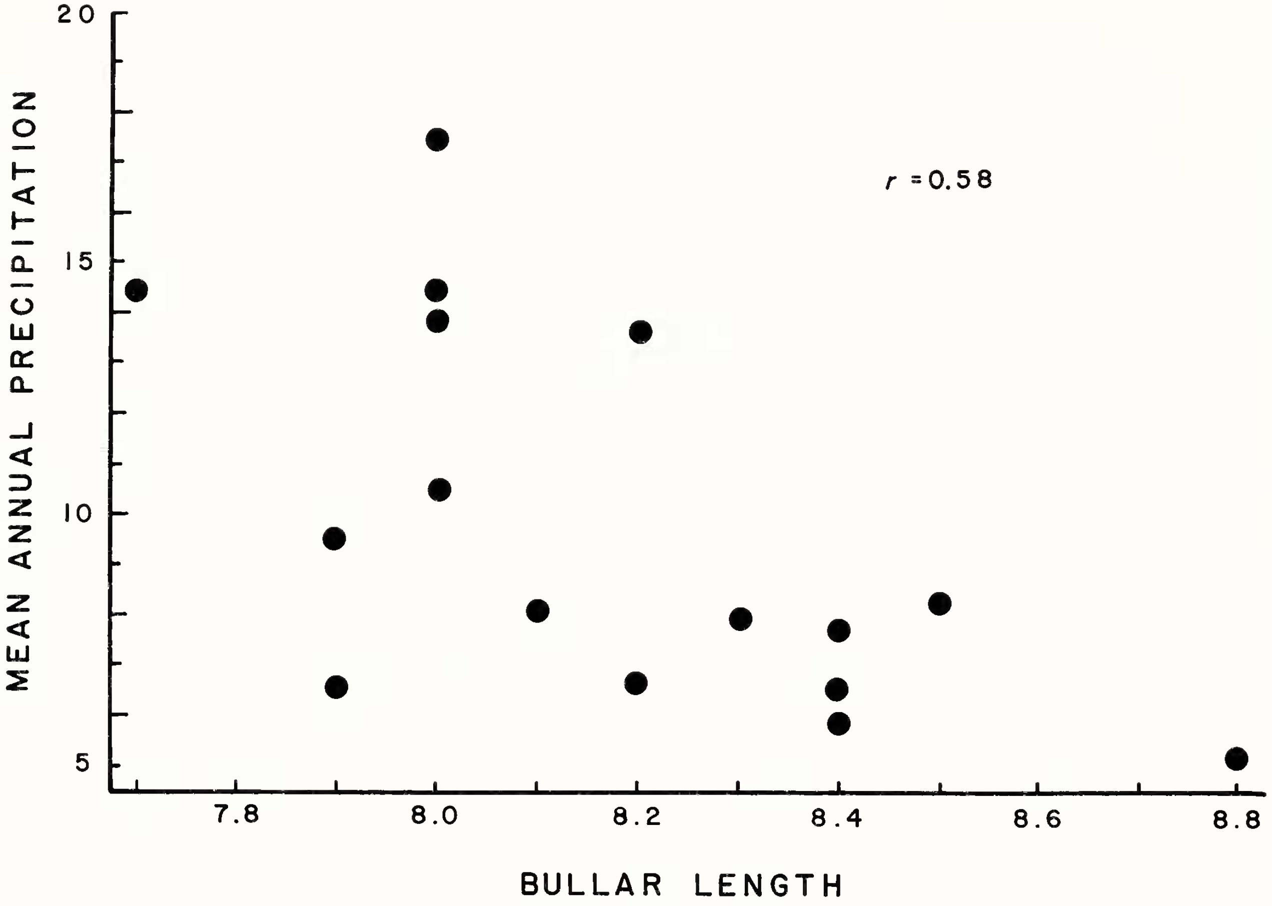

Fig. 12.—Two-dimensional plot, depicting relationship between bullar size (in mm) and mean annual precipitation (in inches), of samples of *Perognathus apache*. $P < 0.05$.

the southward advance of glacial conditions, including the increasingly cooler and wetter climate in the Southwest, caused a southward contraction of the range of the ancestral form. At the height of the glacial pluvial period the population was fragmented into a Chihuahuan Plateau unit and a Southern Plains unit. The most likely barrier separating these populations was the mountains and highlands that transect the Trans-Pecos area of Texas and eastern Chihuahua, and which are continuous with the mountain axis extending southward from the main Rocky Mountain mass.

According to Wells (1970*a*), much of the southern Great Plains region was an open yellow pine-sagebrush parkland during the Wisconsin pluvial period, which is the same type of habitat occupied by some *P. fasciatus* populations today. Northern sagebrush-grassland species, such as *Lagurus curtatus*, have been found in late Pleistocene cave deposits of southeastern New Mexico (Harris, 1970). This supports the hypothesis that a northern plains grassland fauna occupied this region during the Wisconsin pluvial maximum. West of the highland barrier, the other population was isolated in more arid, grassland or desert conditions. Wells (1970*b*) stated that he found no indication that treeless grassland shifted southward into the now arid Chihuahuan Desert during the Wisconsin glacial. Much of the slightly higher plateau regions in this area were vegetated with semiarid grasslands and pinyon-juniper woodlands, habitats that support the denser populations of Apache pocket mice today.

In isolation, these populations, which were already adapted to different environments diverged even more and speciation occurred. The Great Plains isolate was adapted to conditions essentially

Table 12.—*Matrix of taxonomic distance coefficients (average Euclidean distances) for samples of* Perognathus fasciatus, P. apache, *and* P. flavescens. *Refer to Fig. 17, Table 7, or the text for an explanation of the sample codes.*

Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	0.000																				
2	0.571	0.000																			
3	1.136	1.325	0.000																		
4	0.894	1.026	0.693	0.000																	
5	1.849	1.955	1.286	1.363	0.000																
6	1.669	1.775	1.119	1.182	0.678	0.000															
7	1.319	1.276	1.228	0.943	1.611	1.263	0.000														
8	1.452	1.415	1.343	1.094	1.723	1.318	0.477	0.000													
9	1.266	1.319	1.244	0.970	1.285	1.000	0.764	0.860	0.000												
10	1.860	1.974	1.266	1.437	0.943	0.599	1.383	1.362	1.115	0.000											
11	1.174	1.150	1.149	0.907	1.474	1.113	0.628	0.727	0.632	1.220	0.000										
12	1.555	1.607	1.008	1.121	1.116	0.714	0.931	0.967	0.897	0.599	0.849	0.000									
13	1.747	1.600	1.717	1.530	2.125	1.786	0.958	0.971	1.399	1.807	1.184	1.348	0.000								
14	1.074	1.067	1.101	0.952	1.460	1.144	0.621	0.686	0.659	1.226	0.591	0.808	0.976	0.000							
15	1.217	1.260	1.047	0.929	1.283	0.986	0.682	0.670	0.586	1.042	0.615	0.707	1.148	0.431	0.000						
16	1.207	1.034	1.578	1.161	1.960	1.723	0.750	0.867	1.012	1.876	0.896	1.437	1.091	0.835	0.934	0.000					
17	1.158	0.958	1.331	1.068	1.695	1.439	0.691	0.833	0.857	1.550	0.719	1.135	1.029	0.613	0.695	0.579	0.000				
18	1.634	1.424	1.738	1.450	1.916	1.677	0.820	0.881	1.098	1.725	1.038	1.335	0.905	0.928	1.018	0.761	0.709	0.000			
19	1.555	1.370	1.919	1.516	2.367	2.090	1.013	1.039	1.311	2.218	1.248	1.803	1.231	1.224	1.303	0.641	0.976	0.963	0.000		
20	1.879	1.560	2.344	1.938	2.820	2.555	1.599	1.587	1.844	2.719	1.783	2.301	1.680	1.710	1.833	1.134	1.415	1.453	0.909	0.000	
21	1.958	1.629	2.499	2.141	3.032	2.716	1.852	1.851	2.131	2.872	2.024	2.465	1.865	1.920	2.114	1.520	1.711	1.692	1.332	0.894	0.000

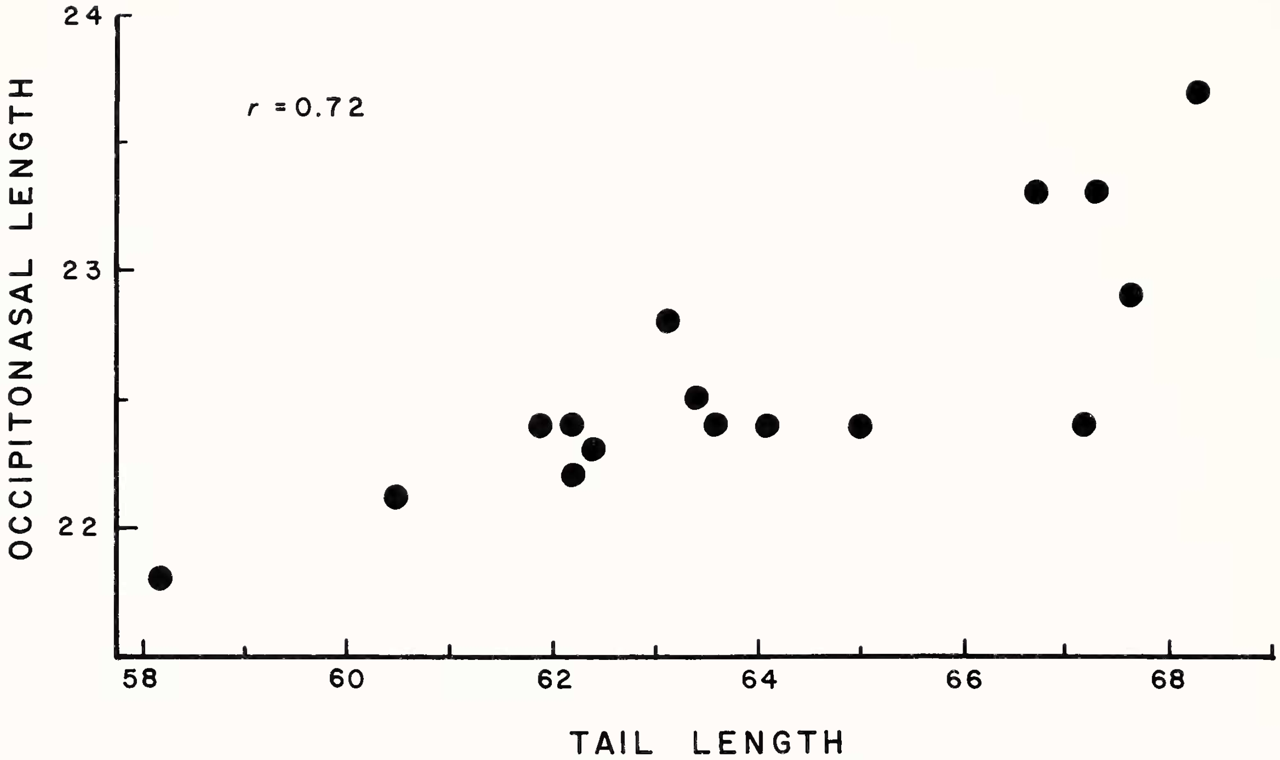

Fig. 13.—Two-dimensional plot, showing relationship between occipitonasal length and length of tail (both in mm), of samples of *Perognathus apache*. $P < 0.01$.

the same as *P. fasciatus* lives under today. The Chihuahuan Desert isolate was adapted to the more arid conditions extant in much of the intermountain region. With the wane of pluvial conditions and the disappearance of woodlands from the central grasslands, both populations began to expand northward. The Rocky Mountain axis of New Mexico and Colorado remained a barrier to pocket mice for some time, and probably prevented contact between the two northward expanding populations. Part of the Chihuahuan isolate's population spread northward as conditions became suitable, but part also remained in place and became progressively more adapted to warmer and more xeric conditions. In time, the Trans-Pecos barrier fell and the Chihuahuan isolate spread onto the southern Great Plains. There, it probably contacted relictual populations of *P. fasciatus*. Perhaps competition with the more xeric adapted *P. flavescens*, coupled with increasingly xeric conditions in the southern Great Plains, hastened the retreat of *P. fasciatus* to the north. Some populations, instead, retreated to higher elevations along the southern Rocky Mountain front of Colorado, such as near La Veta, Silver Cliff, and Colorado Springs, where relict populations are found today. Perhaps others will be found along the Sangre de Cristo range in northern New Mexico. Apache pocket mice pushed northward through the intermountain basins, finally arriving in the Uintah Basin. Olive-backed pocket mice moved into the Uintah Basin from the northeast as forests retreated and conditions became suitable. Primary contact by individuals of these populations is though to be taking place now.

TAXONOMIC CONCLUSIONS

All evidence points to the specific status of *P. fasciatus*. Its different karyotype (which can be used to document interspecific hybrids), different color, and high number of morphometric differences with adjacent populations of Apache and plains pocket mice suggest reproductive isolation. If, as I believe, Apache and olive-backed pocket mice are now making contact for the first time, it is possible that hybridization may occur. However, it seems unlikely that introgression of genes be-

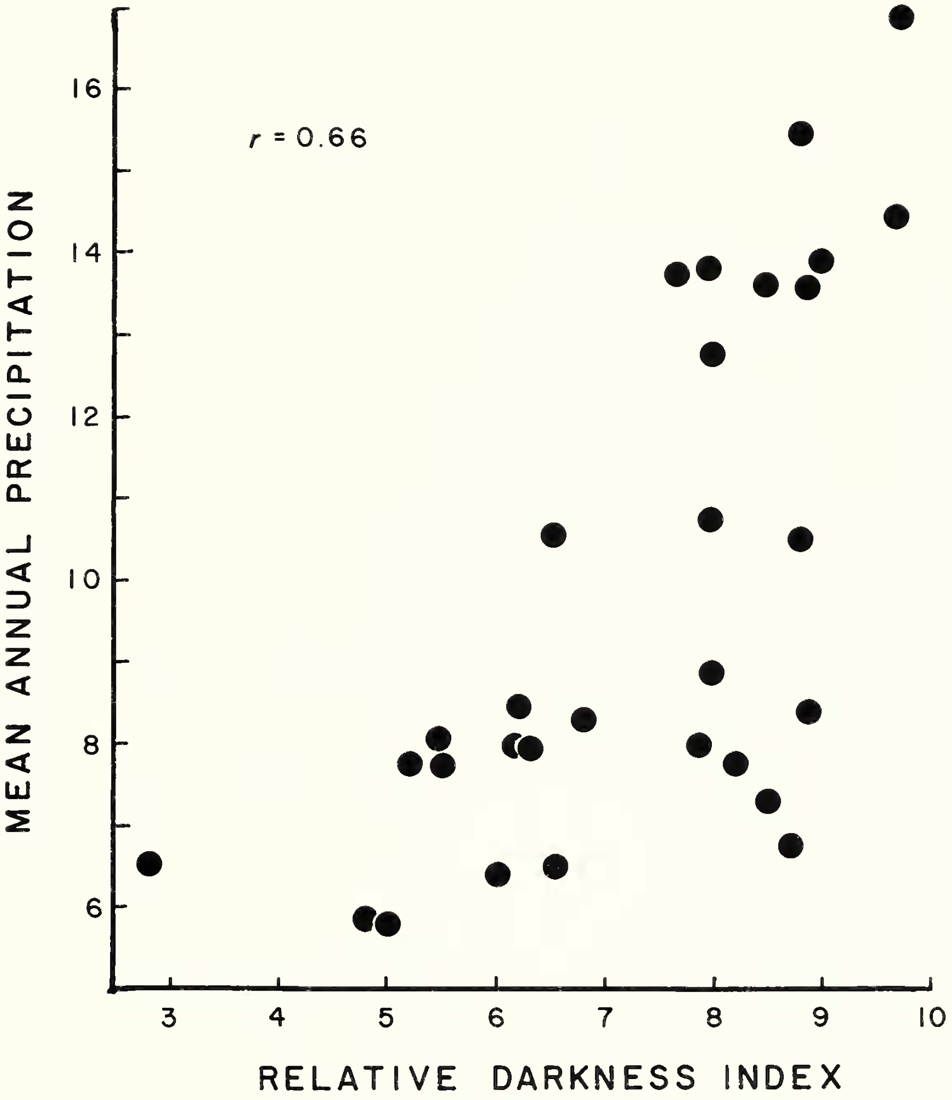

Fig. 14.—Two-dimensional plot, showing relationship between relative darkness index and mean annual precipitation (in inches), of samples of *Perognathus apache*. $P < 0.001$.

tween their populations would occur. This situation warrants further monitoring. Sympatry, without apparent hybridization between olive-backed and plains pocket mice, is widespread in the Great Plains, and confirms their specific integrity in that area.

The evidence suggests that the Apache and plains pocket mice are conspecific. Common color patterns and the close phenetic similarity (including chromosome structure) between adjacent samples point to a close relationship. Greater differences are found between some Apache pocket mouse samples than between *P. f. copei* and the Deming Plains sample of *P. apache*. The approximate 200-km hiatus between nearest collecting localities of the two populations may seem large, but is no greater than some others. The Trans-Pecos gap may be narrowed considerably by additional field work. Both taxa are rarely collected in the southern parts of their ranges, and in my experience, repeated trapping is often necessary to collect one or a few specimens.

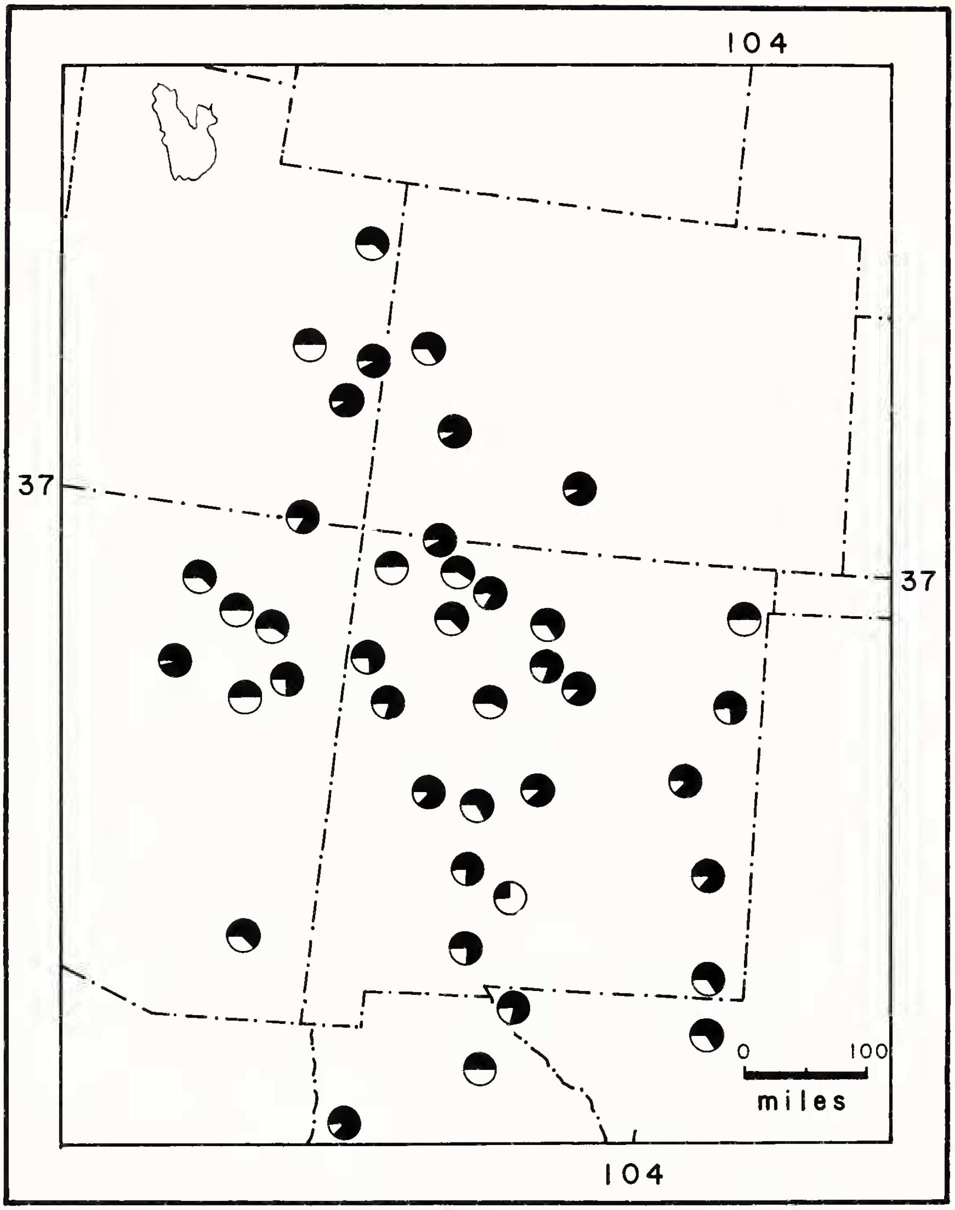

Fig. 15.—Geographic variation in the relative darkness index for samples of *Perognathus apache* and *P. flavescens*. The degree of darkening of the circles represents the relative darkness of the samples. Refer to Table 11 for identification of the samples.

Perognathus flavescens and *P. apache* were named by Merriam (1889), who published their descriptions simultaneously in the same paper. As the first reviser, I have chosen *Perognathus flavescens* as the species name because it has precedence of position (p. 11 versus p. 14, Merriam, 1889), and, more importantly, because the epithet *flavescens* will best ensure stability and universality of nomenclature. In this regard, *apache* appears to be a misspelling of apeches (Greek: discordant, noisy, quarrelsome), probably originating through the French variant, apache (a gangster or thug of Paris).

Fitting the named subspecies of Apache pocket mice into the observed pattern of geographic variation is not too difficult. But, from the original subspecies descriptions, it is clear that most were based primarily on color differences. Paradoxically, the holotypes of *cleomophila*, *caryi*, *relictus*, and *melanotis* are very similar in color, all being darker and richer than the holotype of *apache*. To recog-

Table 13.—*Matrix of similarity coefficients for samples of* Perognathus fasciatus, P. apache, *and* P. flavescens. *Refer to Fig. 19, Table 7, or the text for an explanation of sample codes.*

Sample-	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	1.000																				
2	0.869	1.000																			
3	0.526	0.413	1.000																		
4	0.584	0.468	0.712	1.000																	
5	−0.150	−0.090	−0.068	0.094	1.000																
6	−0.418	−0.432	−0.268	−0.189	0.516	1.000															
7	−0.515	−0.669	−0.048	−0.053	0.025	0.361	1.000														
8	−0.616	−0.760	−0.216	−0.270	−0.264	0.267	0.576	1.000													
9	−0.153	−0.312	−0.443	−0.186	0.257	0.290	0.099	0.029	1.000												
10	−0.561	−0.623	−0.304	−0.549	0.090	0.463	0.361	0.550	0.313	1.000											
11	−0.070	−0.139	−0.025	−0.032	0.115	0.464	0.160	0.108	0.350	0.501	1.000										
12	−0.548	−0.563	−0.060	−0.438	−0.089	0.271	0.501	0.495	−0.053	0.778	0.397	1.000									
13	−0.487	−0.441	−0.208	−0.383	−0.331	−0.123	0.292	0.490	−0.358	0.183	−0.093	0.433	1.000								
14	0.059	−0.045	−0.138	−0.484	−0.183	−0.155	−0.065	0.046	0.058	0.195	0.069	0.281	0.415	1.000							
15	−0.260	−0.458	−0.122	−0.380	0.185	0.171	0.119	0.327	0.267	0.530	0.141	0.339	0.117	0.414	1.000						
16	0.066	0.010	−0.293	0.049	0.343	−0.065	−0.116	−0.277	0.208	−0.284	−0.175	−0.251	−0.178	−0.040	0.176	1.000					
17	−0.067	0.141	−0.135	−0.320	0.194	−0.025	−0.270	−0.424	−0.029	0.106	−0.052	0.068	0.031	0.115	0.220	0.169	1.000				
18	−0.634	−0.480	−0.569	−0.588	0.177	0.074	0.201	0.176	0.071	0.337	−0.158	0.280	0.443	0.068	0.087	0.139	0.339	1.000			
19	−0.262	−0.360	−0.291	−0.096	−0.078	−0.087	0.173	0.247	0.392	−0.142	−0.267	−0.293	−0.038	−0.273	0.092	0.205	−0.248	0.110	1.000		
20	−0.060	0.128	−0.228	−0.043	−0.218	−0.268	−0.336	−0.115	−0.032	−0.476	−0.522	−0.497	−0.189	−0.305	−0.293	0.119	−0.073	−0.100	0.343	1.000	
21	0.129	0.324	−0.187	−0.090	−0.477	−0.354	−0.320	−0.172	−0.312	−0.464	−0.485	−0.414	−0.071	−0.227	−0.572	−0.150	−0.183	−0.039	0.167	0.723	1.000

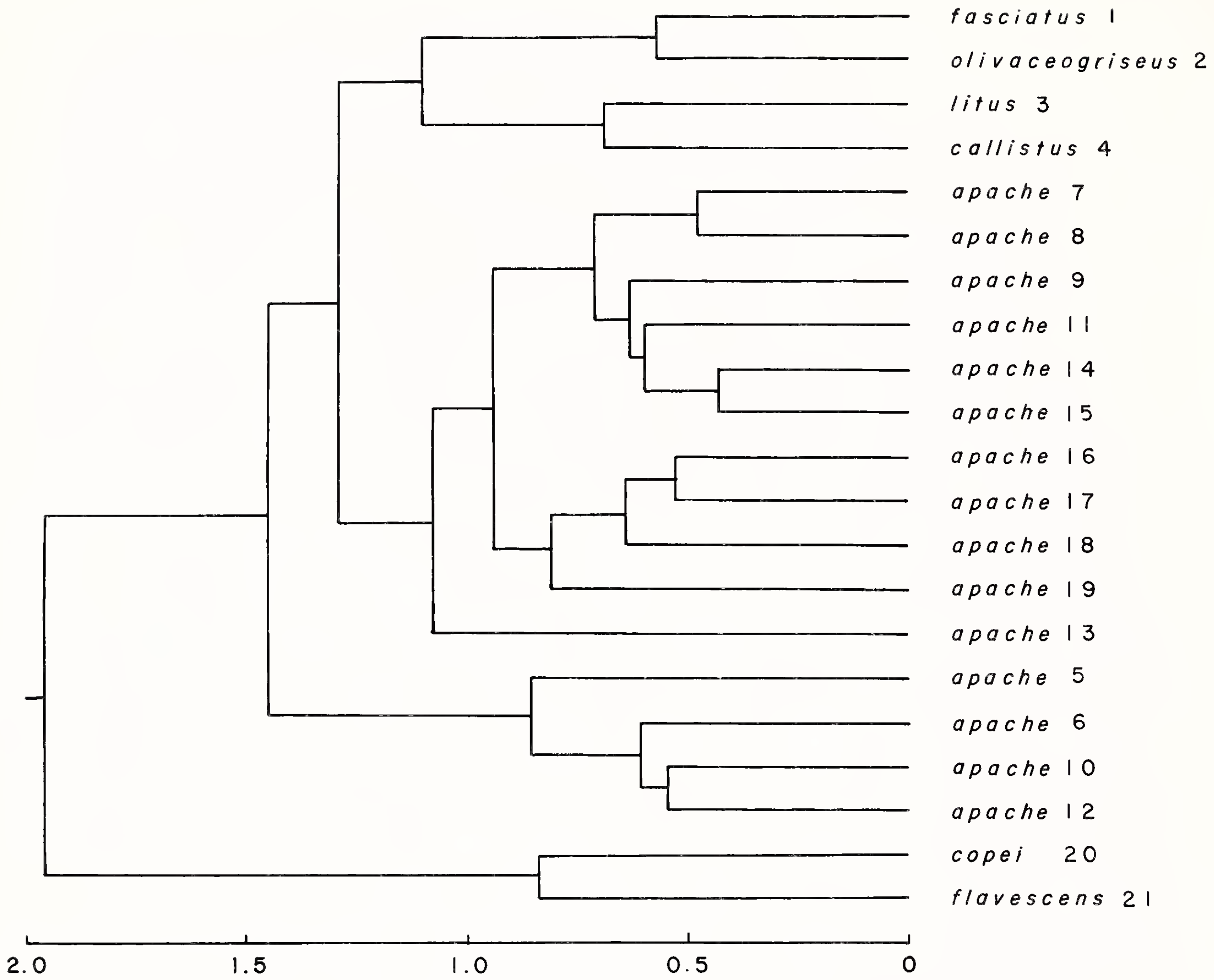

Fig. 16.—Phenogram, based upon taxonomic distances, of samples of the *Perognathus fasciatus* species group. Refer to Fig. 17 or the text for an explanation of sample codes. Grouping was by the unweighted pair-group method using arithmetic averages. The coefficient of cophenetic correlation was 0.77.

nize these and all of the other unique populations (each sample is unique) would require naming a number of new taxa. A more conservative approach seems to be required.

Mice from near Flagstaff differ from *P. flavescens apache* from the lower, drier Painted Desert areas only in color, and even color is quite variable among samples from those areas (Fig. 15). I can see no reason to recognize more than a single subspecies from northeastern Arizona, and regard *P. f. cleomophila* as a junior synonym of *P. f. apache*. The name *P. f. apache* applies only to populations from northern Arizona (Fig. 23) and Utah south of the San Juan River. The southern samples of Apache pocket mice (Fig. 23) comprise a recognizable morphologic unit that is about equally similar to *P. f. copei* and the more northern populations of Apache pocket mice. These samples represent populations previously known as *P. a. apache* (samples 16, 17, and parts of 19), *P. a. melanotis* (part of 19), and *P. a. gypsi* (18). The name *P. flavescens melanotis* is the senior unoccupied name, and *P. f. gypsi* is considered to be a junior synonym. The San Luis Valley sample is divergent structurally, and the name *P. flavescens relictus* is retained for this population. The remaining samples (Fig. 23), extending southeastward from the Uintah Basin through the northwestern quarter of New Mexico, vary clinally in size, but exhibit sufficient morphologic and geographic continutity to make any taxonomic separation highly arbitrary. The name *P. flavescens caryi* applies to these populations.

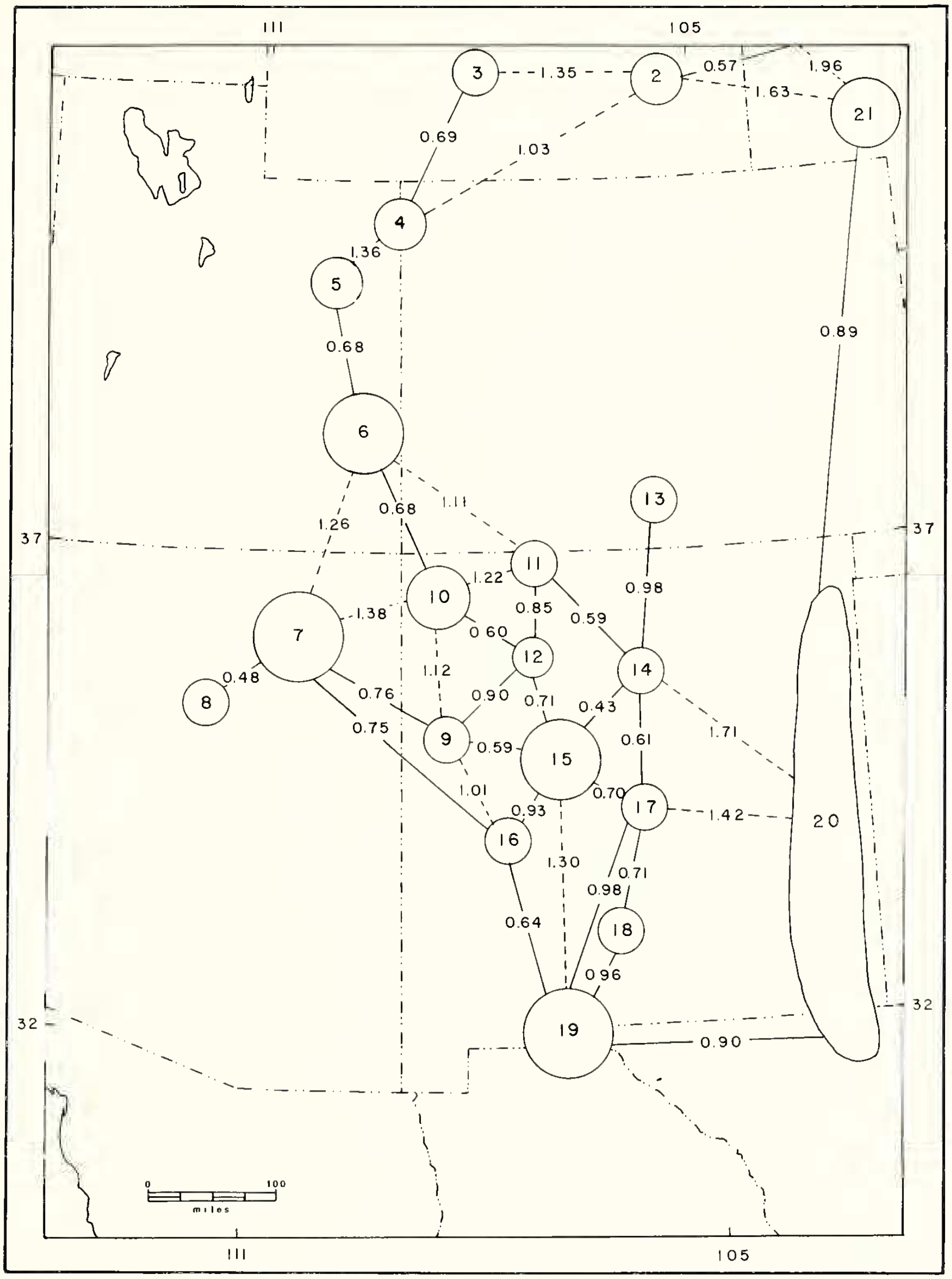

Fig. 17.—Map showing taxonomic distances between adjacent samples of the *Perognathus fasciatus* species group. Lines extending northward from samples 2 and 21 represent intersample comparisons with sample 1. Broken lines connect samples with distance values greater than 1.0. The geographic positions of the samples are only approximations.

SYSTEMATIC ACCOUNTS

Perognathus flavescens apache Meriam, 1889

1889. *Perognathus apache* Merriam, N. Amer. Fauna, 1:14, 25 October.

1918. *Perognathus apache cleomophila* Goldman, Proc. Biol. Soc. Washington, 31:23, 16 May; holotype from Winona, 6,400 ft, Coconino Co., Arizona.

Holotype.—Adult male (age class 5), skin and skull, BS 4253/4984, from near Keam's Canyon, Navajo Co., Arizona; obtained on 22 May 1888 by Jere Sullivan. Skin in good condition; skull in fair condition, bullae damaged.

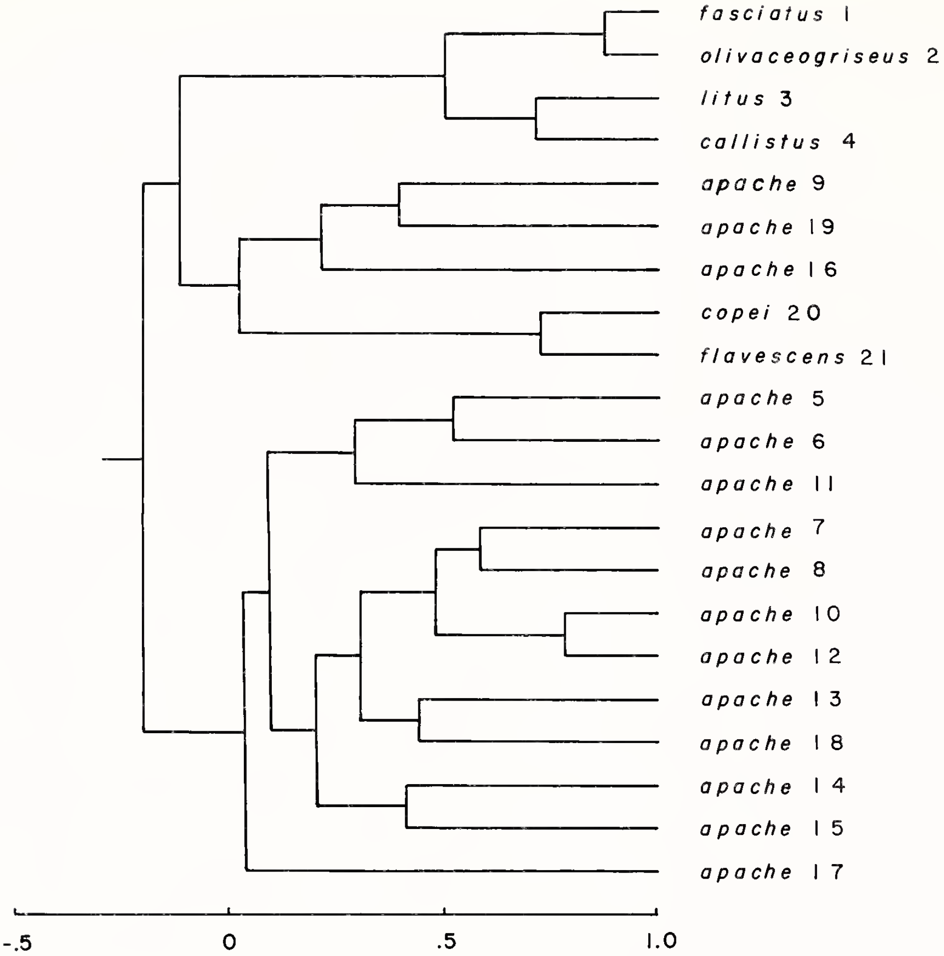

Fig. 18.—Phenogram, based upon coefficients of similarity, of samples of the *Perognathus fasciatus* species group. Refer to Fig. 19 or the text for an explanation of sample codes. The coefficient of cophenetic correlation was 0.73.

Measurements of holotype.—Total length, 140; length of tail, 68; length of hind foot, 18.5 (all external measurements from Merriam, 1889; measurements not recorded on skin tag); occipitonasal length, 24.05; interorbital breadth, 5.10; alveolar length of maxillary toothrow, 3.20; width across maxillary toothrow, 4.60; bullar length, 8.45; length of interparietal, 2.50; width of interparietals, 3.75; length of nasal, 8.70; width of nasals, 2.45; width of rostrum, 4.65; least interbullar distance, 4.00; length of mandibular toothrow, 2.90.

Distribution.—Sandy areas in semiarid grasslands and pinyon-juniper woodlands in northeastern Arizona, north and east of the Mogollon rim, west of the Chuska Mountains, and east of the Coconino Plateau, northward into southeastern Utah east of the Colorado River and south of the San Juan River (Fig. 23).

Diagnosis.—See Table 5, samples 7 and 8, for measurements. Size medium, feet relatively large, ears relatively small. Skull with interparietals very narrow, bullae large, nasals short, rostrum narrow, and interbullar region constricted. Color variable (Table 11, Fig. 15), from lighter and yellower than average, as near Holbrook and Oraibi, to much darker and oranger than average, as near Flagstaff.

Comparisons.—Distinguishable from *P. amplus* and *P. longimembris* by its shorter, nonpenicillate tail and slightly stiffer pelage (length of tail averages greater than 114% of length of head and body in sympatric *P. amplus* and *P. longimembris,* and less

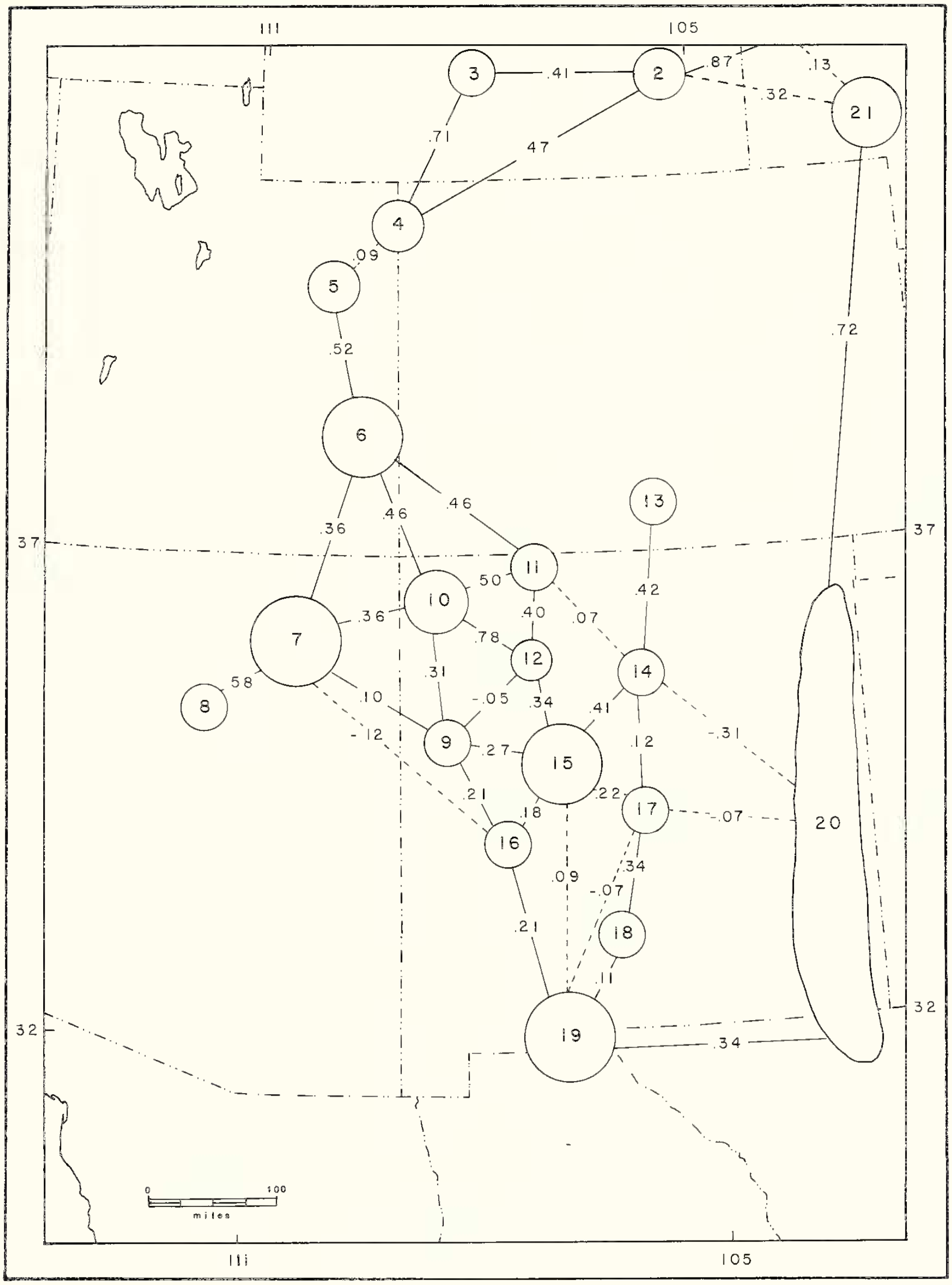

Fig. 19.—Map showing coefficients of similarity between adjacent *Perognathus fasciatus* species group samples. Lines extending northward from samples 2 and 21 represent intersample comparisons with sample 1. Broken lines connect samples with similarity values of less than 0.1, and samples of sympatric species. The geographic positions of the samples are only approximations.

than 95% in *P. f. apache*). Body size about 18% larger than sympatric *P. flavus*, with a relatively longer tail (length of tail averages 86% of length of head and body in *P. flavus*) and with smaller postauricular spots that contrast less with dorsal color. Skull about 11% longer than that of *P. flavus*, with relatively smaller bullae (length of bullae averages 40% of occipitonasal length in *P. flavus*, and 37% in *P. f. apache*), and wider interorbital region (interorbital breadth averages greater than 5.1 mm in *P. f. apache* and less than 4.5 mm in *P. flavus*). Size somewhat smaller than adjacent *P. f. caryi* popu-

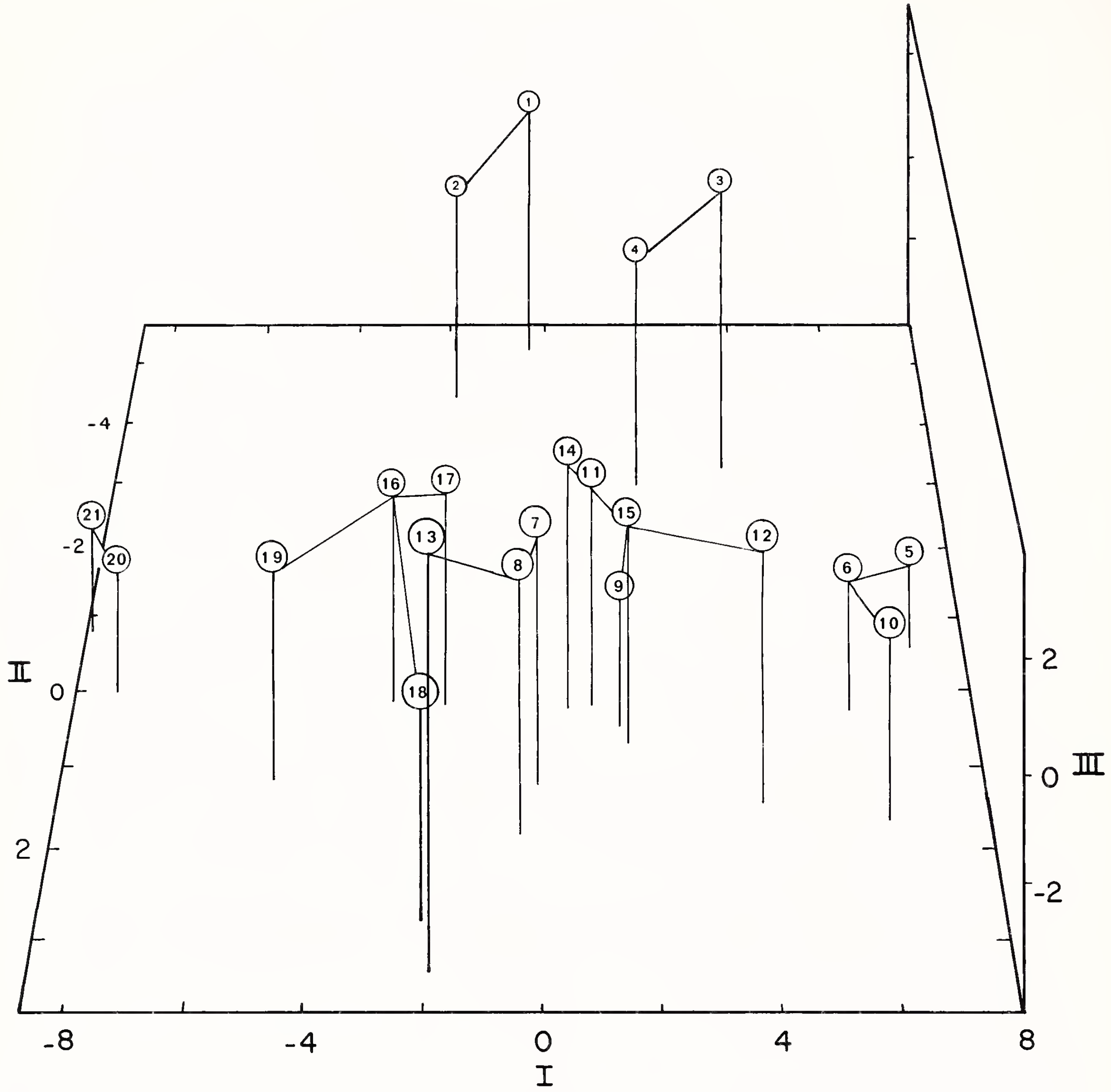

Fig. 20.—Three-dimensional plot of the first three principal components, derived from the matrix of similarity, for samples of the *P. fasciatus* species group. Lines between samples connect samples sharing the same centroid. The sample codes are defined in the text and in Table 7.

lations, with shorter skull, smaller interparietal dimensions, and smaller teeth (Tables 5 and 8). Size larger than *P. f. melanotis*, with relatively longer tail and shorter nasals.

Remarks.—The type locality was listed as Apache Co. by Merriam (1889), but is actually in Navajo Co. The holotype averaged larger in most dimensions than typical specimens of *P. f. apache*, but was within the range of measurements for the Keam's Canyon sample. *P. f. apache* populations averaged largest in measurements in the north, near the San Juan River, and smallest in the south. Spec-

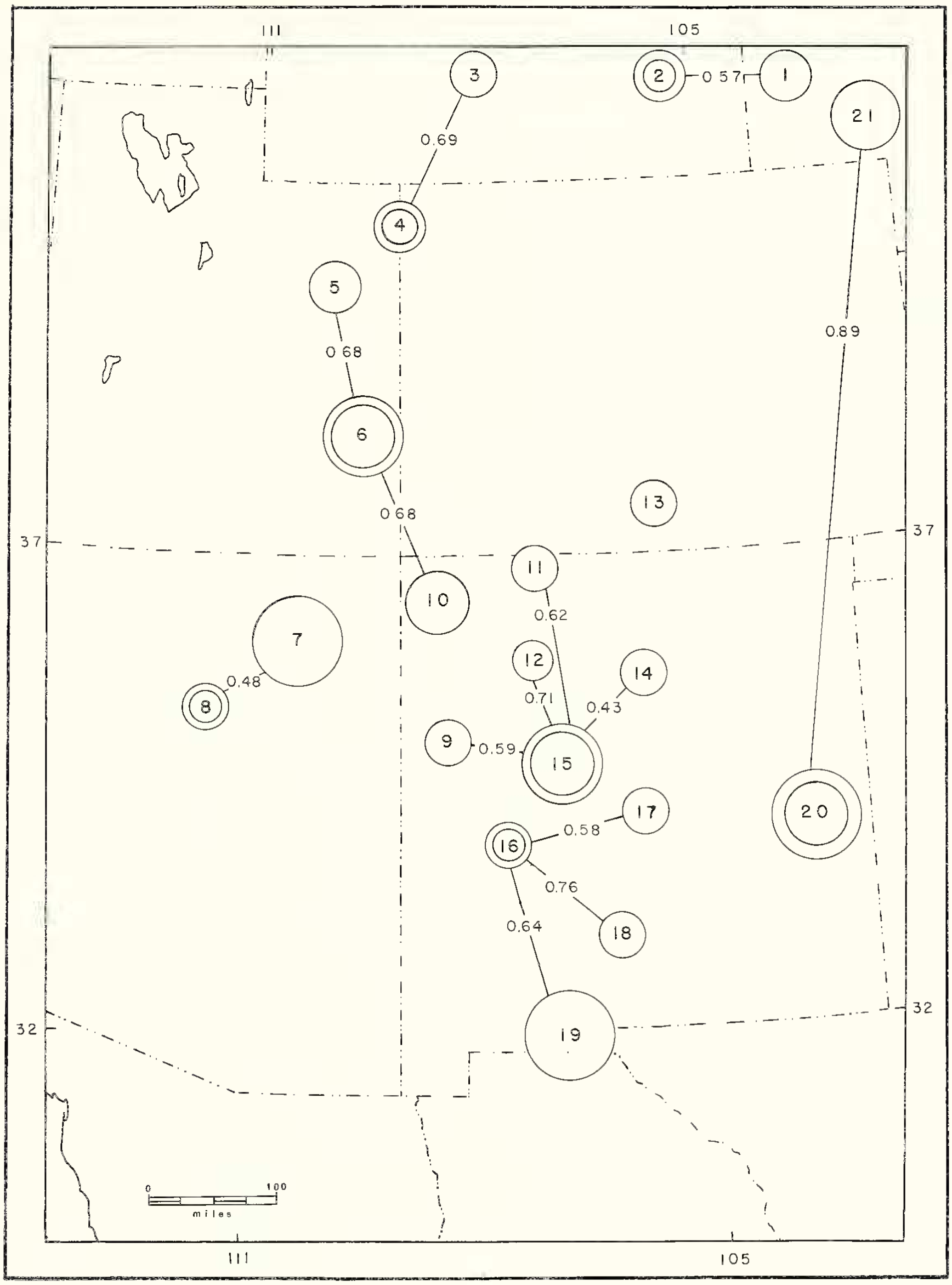

Fig. 21.—Map showing the geographic positions of the samples belonging to the seven centroids extracted from the matrix of taxonomic distances. Concentric circles depict the centroid samples. Sample 13 was placed with the Arizona samples (centroid 8).

imens from southern Utah and adjacent Arizona are somewhat intermediate to *P. a. caryi* from northwestern New Mexico, and their populations are probably continuous in the Four Corners area. Specimens from near Holbrook and Adamana approach *P. f. caryi* of the Gallup sample in size and proportions and are somewhat similar to *P. f. melanotis* from the San Augustine Plains. Cockrum (1960) assigned two specimens from 3 and 2 mi W Wupatki, Coconino Co., Arizona, to *P. a. cleomophila*. These specimens represent *P. amplus cineris* Benson, 1933.

Table 14.—*Matrix of classification, based upon the discriminant functions of 29 morphometric traits. Values indicate the number of individuals classified into each group. See text for further explanation.*

Samples	Classification groups											
	2	3	5	6	7	8	10	13	15	18	19	20
1. *Perognathus fasciatus fasciatus*	7	—	—	—	—	—	—	—	—	—	—	—
2. *Perognathus fasciatus olivaceogriseus*	15	—	—	—	—	—	—	—	—	—	—	—
3. *Perognathus fasciatus callistus* and *litus*	—	40	—	—	—	—	—	—	—	—	—	1
5. *Perognathus apache* Uintah Basin	—	—	53	2	1	—	1	—	—	—	—	—
6. *Perognathus apache* Moab	—	—	1	17	1	—	1	—	—	—	—	—
7. *Perognathus apache* Painted Desert	—	1	—	—	28	1	2	—	2	6	1	—
8. *Perognathus apache* Flagstaff	—	—	—	—	1	23	1	—	2	1	2	1
9. *Perognathus apache* Gallup	—	—	—	—	1	1	1	—	—	—	—	—
10. *Perognathus apache* San Juan Basin	—	—	1	4	2	1	21	—	1	—	—	—
11. *Perognathus apache* Canyon Largo	—	1	—	4	—	3	3	—	5	—	4	1
12. *Perognathus apache* Estrella	—	—	—	1	3	2	5	—	2	—	—	—
13. *Perognathus apache* San Luis Valley	—	—	—	—	—	—	—	13	—	—	—	—
14. *Perognathus apache* Santa Fe	1	—	—	—	1	3	1	2	7	—	1	—
15. *Perognathus apache* Rio Grande Valley	—	—	—	—	3	4	6	1	36	3	4	—
17. *Perognathus apache* Gran Quivira	—	—	—	—	—	—	—	—	3	1	5	—
18. *Perognathus apache* White Sands	—	—	—	—	2	1	1	—	1	31	1	—
19. *Perognathus apache* Deming and San Augustine	—	—	—	—	1	4	—	—	1	1	23	1
20. *Perognathus flavescens* and *P. f. copei*	—	—	—	—	—	—	—	—	—	1	1	13

Records of occurrence.—Specimens examined, 187, distributed as follows: ARIZONA. *Apache Co.:* Four Corners, 1 (UIMNH); Chin Lee, 5,600 ft, 3 (BS); Zuni Well, 7.5 mi N Adamana, 5,337 ft, 1 (MVZ). *Coconino Co.:* 2 mi S Endische Spring, Navajo Mountain, 3 (MVZ), 1 (TCWC); 5 mi S Navajo Mountain, 1 (MVZ); Page, 1 (UIMNH); 0.5 mi NW Page, 1 (UIMNH); 0.5 mi S Page, 7 (UIMNH); Salt River Project, Navajo Generating Plant Site, Page, 4,520 ft, 4 (MNA); 6 mi SE Page, 1 (MNA); 19 mi SW Page (hwy. 189), 1 (UIMNH); 2 mi N, 1 mi E Bitter Springs, 3 (UIMNH); Cedar Ridge, 6,000 ft, 1 (MVZ); 3 mi above mouth, Cedar Ranch Wash, 3 (BS); Tuba City, Painted Desert, 1 (BS), 1 (MVZ); Moa Ave, 1 (BS), 10 (MVZ); Moenkopi Wash, 12 mi above mouth, 4,500 ft, 3 (BS); 2.5 mi S, 2 mi E Moenkopi, 5,050 ft, 6 (UIMNH); 2.5 mi SE Moenkopi, 4,900 ft, 4 (UIMNH); 5 mi S, 2 mi E Moenkopi, 5,500 ft, 4 (UIMNH); 5 mi N Cameron, 1 (UIMNH); 4.5 mi N Cameron, 1 (UIMNH); 3 mi S Visitor Center, Wupatki National Monument, 5,000 ft, 4 (MNA), 1 (UIMNH); 4 mi W Winona, 1

Table 15.—*Mean scores for canonical variables for samples of* Perognathus fasciatus, P. apache, *and* P. flavescens.

Samples	Canonical variables				
	I	II	III	IV	V
1. *Perognathus fasciatus fasciatus*	−1.667	−4.449	2.163	−0.400	1.074
2. *Perognathus fasciatus olivaceogriseus*	−1.772	−4.215	1.878	−0.244	2.057
3. *Perognathus fasciatus callistus* and *litus*	−2.802	−2.722	−1.040	0.841	−0.733
5. *Perognathus apache* Uintah Basin	−3.107	1.489	0.207	−0.852	−0.428
6. *Perognathus apache* Moab	−1.607	1.439	0.908	0.372	0.235
7. *Perognathus apache* Painted Desert	0.745	0.594	−1.648	0.329	0.115
8. *Perognathus apache* Flagstaff	2.094	0.160	0.659	0.854	−0.190
9. *Perognathus apache* Gallup	0.883	1.267	0.389	0.888	0.265
10. *Perognathus apache* San Juan Basin	0.283	1.668	0.601	1.960	0.373
11. *Perognathus apache* Canyon Largo	0.740	−0.147	0.361	0.708	0.357
12. *Perognathus apache* Estrella	0.642	0.787	−0.057	1.396	−0.283
13. *Perognathus apache* San Luis Valley	3.942	−1.416	0.954	−1.057	−2.710
14. *Perognathus apache* Santa Fe	1.411	−0.816	1.272	0.066	−0.259
15. *Perognathus apache* Rio Grande Valley	1.188	−0.062	0.756	−0.184	−0.139
17. *Perognathus apache* Gran Quivira	0.680	−1.056	−0.205	−1.020	0.493
18. *Perognathus apache* White Sands	1.636	0.459	−0.953	−0.724	1.049
19. *Perognathus apache* Deming and San Augustine	1.284	−0.516	−0.290	−1.244	0.555
20. *Perognathus flavescens copei* and *P. f. flavescens*	0.897	−1.881	0.357	−0.614	1.461
Cumulative % of total dispersion	39.75	64.21	73.49	81.83	88.82

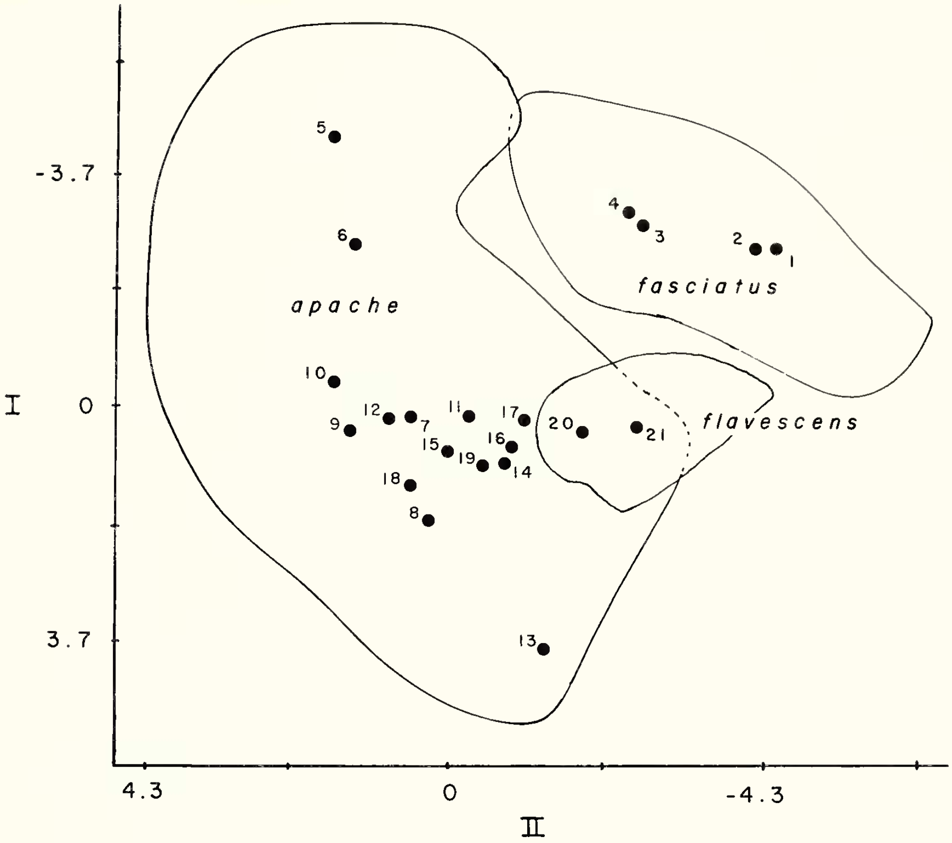

Fig. 22.—Two-dimensional plot of the first two canonical variables for individuals of the *P. fasciatus* species group. Circles mark the positions of the sample means, whereas the lines encompass the distribution of the individual cases for each taxon. To prevent visual confusion, the positions of the individual cases are not shown. Refer to the text or Table 7 for an explanation of the sample codes.

+ chromosomes (MSB); 3 mi NW Winona, 6,400 ft, 27 (BS); Winona, 6,400 ft, 7 (MVZ); Grand Falls, Little Colorado River, 2 (UCM); 1 mi SE Grand Falls, 1 (MVZ); 30 mi NE Flagstaff, 1 (BS); 9 mi E Flagstaff, 1 (BS); Walnut, 5 mi from Turkey Tank, 4 (BS). *Navajo Co.:* 11 mi N Kayenta, 4 (UIMNH); 4.5 mi N, 1 mi E Kayenta, 2 (UIMNH); 1 mi E Kayenta, 5 (UIMNH); Dogoszhi Biko Canyon, mouth of Water Lily Canyon, 11 (MNA); Keam's Canyon, 7 (BS), 20 (MVZ), 8 (UIMNH); Oraibi, 6,000 ft, 7 (BS), 5 (MVZ); Holbrook, 2 (BS); 0.5 mi S, 3 mi E Holbrook, 1 (UIMNH); Winslow, Painted Desert, 5,326 ft, 1 (BS), 3 (UMMZ); 2 mi N, 2 mi E Winslow, 1 (UIMNH); 2 mi E Winslow, Little Colorado River, 1 (BS); Winslow, N side river, 1 (BS). UTAH. *San Juan Co.:* Navajo Mountain Trading Post, 5 mi SE Navajo Mountain, 1 (MVZ).

Additional records.—ARIZONA. *Apache Co.:* Canyon de Chelley (Cockrum, 1960). *Coconino Co.:* Tappan Spring, 4,500 ft (Cockrum, 1960). *Navajo Co.:* Walpi (Cockrum, 1960).

Perognathus flavescens caryi Goldman, 1918

1918. *Perognathus apache caryi* Goldman, Proc. Biol. Soc. Washington, 31:24, 16 May.

Holotype.—Adult male (age class 4), skin and skull, BS 148206, from 8 mi W Rifle, Garfield Co., Colorado; obtained on 4 October 1906 by M. Cary. Both skin and skull in good condition.

Measurements of holotype.—Total length, 154; length of tail, 73; length of hind foot, 21; occipitonasal length, 25.15; interorbital breadth, 5.60; alveolar length of maxillary toothrow, 3.50; width across maxillary toothrows, 4.65; bullar length, 9.00; width across bullae, 13.40; length of interparietal, 3.35; width of interparietals, 4.15; length of nasal, 9.30; width of nasals, 2.30; width of rostrum, 4.35; least interbullar distance, 4.20; length of mandibular toothrow, 3.15.

Distribution.—Usually in sandy areas in semiarid grasslands and pinyon-juniper associations, from near Val Verde in the Rio Grande Valley, northward to at least the Rio Chama; and from the upper Pecos Valley and the Rio Grande Valley westward to Gallup and the Chuska Mountains, all in New Mexico; northward from the Four Corners area through western Colorado and eastern Utah into the

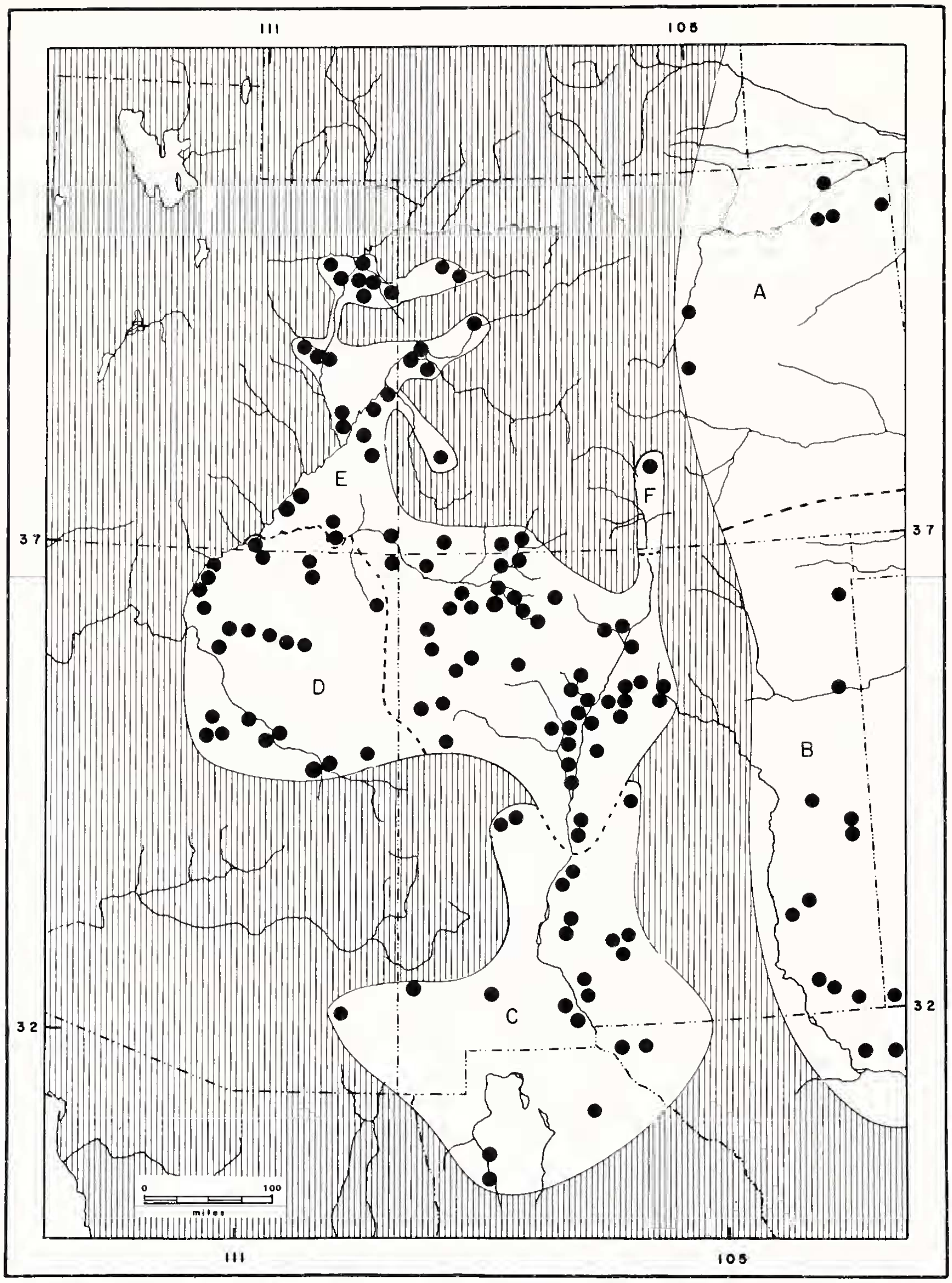

Fig. 23.—Map showing geographic range of the intermountain races of *Perognathus flavescens*, and portions of the ranges of two of the Great Plains races. Circles represent localities from which specimens were examined. To prevent crowding, single circles represent two or more localities that partially overlapped on the map. A = *P. f. flavescens;* B = *P. f. copei;* C = *P. f. melanotis;* D = *P. f. apache;* E = *P. f. caryi;* F = *P. f. relictus*.

Uintah Basin, at least to the Duchesne and White rivers. Not known from west of the Colorado and Green rivers south of the city of Green River (Fig. 23).

Diagnosis.—See Table 5, samples 5, 6, 9, 10, 11, 12, 14, and 15, for measurements. Size of most characters averaging from medium to large, and varying clinally, being largest in the north (sample 5) and smallest in the southeast (sample 14). Skull with relatively constricted interbullar region and with narrow interparietals. Color variable, lightest and palest in the San Juan Basin and near Green

River, Utah, and darkest and richest at higher elevations (Table 11, Fig. 15).

Comparisons.—See account of *P. f. apache* for remarks on distinguishing *P. flavus*. Size smaller and with a relatively shorter, nonpenicillate tail than *P. parvus; P. parvus* is generally tannish-gray or tannish colored (not yellowish-orange), and has less contrasting postauricular spots than *P. flavescens;* occipitonasal length less than 25.5 mm in *P. flavescens*, but greater than 26.5 mm in *P. parvus*. Differs from *P. fasciatus callistus* in larger size, relatively longer tail, and yellowish-orange, rather than olive-yellow, lateral line; interparietal of *P. f. caryi* longer, rostrum wider and interbullar region narrower than *P. f. callistus;* mandibular toothrow longer, M^1 wider, and M_1 larger in *P. f. caryi*. Skull larger, but interorbital region narrower and interparietals larger than *P. f. relictus;* premolars and molars larger than *P. f. relictus*. Size larger and tail relatively longer than *P. f. melanotis;* skull longer and interparietals shorter and narrower than *P. f. melanotis*.

Remarks.—This is the most variable of the intermountain races of *P. flavescens*. The dominant trend is the north-south size cline. Specimens from Gallup are somewhat intermediate to *P. f. apache* and also show some similarity to *P. f. melanotis* from the San Augustine Plains. The Uintah Basin population is found on a variety of substrates, but most others appear to be limited to loose sands. Durrant (1952) thought that the Uintah Basin population represented an undescribed subspecies. Size averages slightly larger in the Uintah Basin population, but it is, overall, similar to *P. f. caryi* from south of the Tavaputs Plateau, and subspecific recognition does not seem warranted.

A specimen from San Antonio Mountains, N Tres Piedras, Rio Arriba Co., New Mexico, listed as this species by Findley et al. (1975), is *P. flavus*.

Records of occurrence.—Specimens examined, 448, distributed as follows: Colorado. *Garfield Co.:* 7 mi W Rifle, 2 (BS); 8 mi W Rifle, 2 (MVZ). *La Plata Co.:* 9 mi S Ignacio, 1 (UU). *Mesa Co.:* Sieber Ranch, Little Dolores Creek, 1 (UCM); 0.25 mi E Colorado National Monument, 1 (DCBML); 0.5 mi E Grand Junction Entrance Station, Colorado National Monument, 2 (UCM); Fruita, 1 (BS); Badger Wash, 8 (DCBML); State Line, 1 (MVZ). *Montezuma Co.:* Morfield Mesa, Mesa Verde National Park, 2 (KU). *Montrose Co.:* Coventry, 1 (BS); Bedrock, 3 (UCM). *Rio Blanco Co.:* 17 mi W Meeker, 1 (DCBML); 7 mi N, 19 mi E Rangely, 2 (DCBML). New Mexico. *Bernalillo Co.:* 2 mi N Albuquerque, 2 (MSB); West Mesa, W Albuquerque near Lava Flow, 1 (MSB); 2 mi N, 5.5 mi W Albuquerque, 2 (MSB); 2.5 mi N, 6 mi W Albuquerque, 2 (MSB); 5 mi W Albuquerque, 3 (MSB); W Albuquerque, E side Rio Puerco Valley, S U.S. 66, 2 (MSB); 18 mi W Albuquerque, Puerco Valley, 3 (MSB); 14 mi W Albuquerque, 24 (MSB), 2 + chromosomes (MSB); 16 mi W Albuquerque, 2 (UIMNH); 4.8 mi N, 14 mi W Albuquerque, 1 (MSB); 14.7 mi N, 3 mi E Suwanne, 2 (MSB); 2.5 mi S, 7.5 mi E Suwanne, 3 (MSB); 0.25 mi S, 10.2 mi W Isleta, 12 (MSB); 2.2 mi S, 10.5 mi W Isleta, 1 (MSB). *McKinley Co.:* Gallup, 3 (BS); Wingate, 4 (BS); 3 mi N, 2 mi W Estrella, 7 (MSB); 4 mi N, 2 mi W Estrella, 8 (MSB); 3 mi N Crownpoint, 1 (MSB). *Rio Arriba Co.:* Stinking Springs Lake (Burford Lake), 1 (BS); 10 mi W Lindrith along Canyada Larga, 4 (MSB); River mile 165, River Island, San Juan River, 1 (UU); River mile 166, San Juan River, 1 (UU); Rio Ojo Caliente, 1.5 mi E, 1 mi N Chili, 2 (MSB); Espanola, 9 (BS); 5 mi E Abiquiu, 1 (BS); 3.5 mi S junction U.S. 285 and N.M. 30, on 30, T20N, R8E, 1 (MSB). *Sandoval Co.:* 5 mi S, 3 mi E Domingo, 2 (MSB); San Felipe Indian Reservation, sec. 2, T13N, R5E, 1 (MSB); Jemez, 1 (BS); 0.25 mi S, 1 mi W San Ysidro, 1 (MSB); 6 mi S, 4.5 mi W San Ysidro, 9 (MSB); 1 mi SW Santa Ana Pueblo, 2 (MSB), 4 (CM), 12 + chromosomes (MSB); 4.5 mi N, 14 mi W Alameda, 6 (MSB). *San Juan Co.:* Chaco Wash, 6 mi E, 14 mi S Shiprock, 43 (MSB); Newcomb, 5 mi N, 6 mi E, 1 (MSB); Newcomb, 1 (MSB); Gallego Canyon, 7.5 mi S, 5 mi E Farmington, 1 (MSB); Gallego Canyon, 7.5 mi S, 4 mi E Farmington, 1 (MSB); 7 mi S, 6 mi W Bloomfield, sec. 4, T27N, R12W, 2 (MSB); 13 mi S, 11 mi E Farmington, 3 (MSB); 3 mi S, 3 mi E Farmington, 2 (MSB); 10 mi S, 7 mi E Farmington, 1 (MSB); 16 mi S, 1 mi W Farmington, sec. 17, T26N, R13W, 2 (MSB); upper Benito Canyon, 1 (UU); Lucero Place, sec. 17, T31N, R7W, 1 (MSB); Pine River Road, sec. 9, T31N, R7W, 1 (MSB); Canyon Largo, sec. 22, T29N, R9W, 7 (MSB); 3 mi S, 3 mi E Blanco, 1 (MSB); Canyon Largo at Fresno Canyon, sec. 33, T28N, R8W, 27 (MSB); 0.5 mi ESE Four Corners boundary marker, 2 (MSB); 5.5 mi N, 1.5 mi W Waterflow, 1 (MSB); El Huerfano, 0.5 mi SE base, 1 (MSB); Chaco Canyon National Monument, 2 (MSB). *San Miguel Co.:* Pecos, 4 (BS); 3 mi S Pecos, 13 (BS). *Santa Fe Co.:* Rio Tesuque, sec. 14, T18N, R9E, 1 (MSB); NW Santa Fe Airport, 2 mi W Sewage Disposal Plant, 1 (MSB); Santa Fe, 1 (BS); Galisteo Creek, 1 mi E U.S. 85, sec. 31, T15N, R7E, 1 (MSB); 1 mi W Cerillos on Galisteo Creek, 1 (MSB); Galisteo Creek, 1 mi E Galisteo R.R. Station, sec. 26, T14N, R8E, 1 (MSB); Glorieta, 2 (BS); San Pedro, 1 (BS). *Socorro Co.:* 1 mi N Pope, 2 mi S Lava Mesa, 1 + chromosomes (MSB); Lava Mesa, 2 mi SE San Marcial, 1 (MVZ); 0.5 mi S, 2 mi W Bernardo, 2 (MSB); 4 mi E Escondida, 2 (MSB); 2 mi N, 4.5 mi E Socorro, 3 (MSB); Lava Mesa, S of Clyde, 1 (MBZ). *Valencia Co.:* 2 mi E Valencia, 1 + chromosomes (MSB); 1.5 mi S, 5 mi W Los Lunas, 1 (MSB); 2 mi S, 8.5 mi W Los Lunas, 4 (MSB); 2 mi W Los Chavez, 2 (MSB); 7 mi W Belen, 1 (MSB); Zuni Mountains, 2.5 mi E El Moro, 1 (LACM). Utah. *Duchesne Co.:* S Myton Bench, 3 mi SE Myton, 3 (UU); Myton Bench, 5 mi SE Myton, 16 (UU). *Emery Co.:* 16 mi NW Green River, 1 (CM); Gunnison Valley, W side Green River, 7.6 mi N Green River (city), 4,200 ft, 2 (UU). *Grand Co.:* Castle Valley, 10 mi NE Moab, 5,000 ft, 5 (UU); Castle Valley, 8 mi NE Moab, 1 (UU); 1 mi E Green River (city), 4,080 ft, 8 (UU); 1 mi SE Dewey Bridge, S side Colorado River, 4,500 ft, 1 (UU); 3 mi SE Dewey, S side River, 4,810 ft, 1 (UU); 4 mi SE Dewey, 5,000 ft, 1 (UU); Big Flat, sec. 21, T26N, R19E, 6,000 ft, 2 (UCM). *San Juan Co.:* S end Gray's Pasture, sec. 32, T27S, R19E, 5,960 ft, 7 (UCM); Willow Flat, sec. 6, T28S, R19E, 6,040 ft, 4 (UCM); sec. 5, T27S, R19E, 6,050 ft, 1 (UCM); NE Corner Gray's Pasture, sec. 22, T26S, R19E, 6,000 ft, 1 (UCM); Chester Canyon at Beef Basin Rd., sec. 7, T31S, R19E, 5,280 ft, 7 (UCM); W of Squaw Butte, sec. 25, T30S, R19E, 5,040 ft, 3 (UCM); S of Squaw Butte, sec. 30, T30S, R20E, 5,040 ft, 2 (UCM); SW Cave Spring, sec. 29–30, T30S, R20E, 5,000 ft, 4 (UCM); Canyon Lands National Park, sec. 15, T27S, R19E, 5,900 ft, 1 (MMNH); Dry Valley (=Hatch Crossing, about 30 mi N Monticello), 1 (BS); 1 mi S Kern Spring, 5 + chromosomes (MSB); Highway 160, 25 mi N Monticello, 6,100 ft, 1 (UU); Bluff, 4,400 ft, 1 (MVZ); 1 mi N Bluff, 4,500 ft, 1 (UU); Noland's Ranch, San Juan River, 1 (BS); Johns Canyon, 5,150 ft, 1 (UU); 119 mi N Lee's Ferry, 3 (UU); 121 mi N Lee's Ferry, 2 (UU); 142 mi N Lee's Ferry, 2 (UU). *Uintah Co.:* Evacuation Creek, 2 mi S White River, 1 (MSB), 2 + chromosomes (MSB); S shore White River, 3 mi S Bonanza, 1 (MSB), 1 + chromosomes (MSB); Evacuation Wash, 4 mi NE Rainbow, 5,600 ft, 3 (UU); 2 mi NE Rainbow, 5,800 ft, 2 (UU); Brown's Corral, 20 mi S Ouray, 6,250 ft, 4 (UU); Willow Creek, 25 mi S Ouray, 5,250 ft, 2 (UU); White River, 2 mi W upper White River Crossing, 14 mi N Dragon, 5,000 ft, 1 (UU); confluence of Green and White rivers, 1 mi S Ouray, 4,654 ft, 2 (UU); 2 mi S Ouray, 4,800 ft, 2 (UU); 1.5 mi S, 1 mi E Ouray, 7 (MSB); 2 + chromosomes (MSB); 1.5 mi E Ouray, N White River, 20 (MSB), 2 + chromosomes (MSB); Pariette Bench, 4,700 ft, 6 mi SW Ouray, W Green River, 1 (CM).

Additional records.—COLORADO. *Mesa Co.:* 0.25 mi W Red Canyon Overlook, Colorado National Monument, 6,400 ft; 0.25 mi SE East Entrance Ranger Station (Armstrong, 1972). NEW MEXICO. *Valencia Co.:* near Laguna (Bailey, 1932). UTAH. *San Juan Co.:* 0.5 mi N Bluff, 4,400 ft (Durrant, 1952); River View (Durrant, 1952).

Perognathus flavescens relictus Goldman, 1938

1938. *Perognathus apache relictus* Goldman, J. Mamm., 19:495, 14 November.

Holotype.—Adult male (age class 4), skin and skull, BS 150768, from Medano Ranch, 15 mi NE Mosca, Alamosa Co., Colorado; obtained on 2 November 1907 by M. Cary. Both skin and skull in good condition.

Measurements of holotype.—Total length, 137; length of tail, 68; length of hind foot, 19.0; occipitonasal length, 22.70; interorbital breadth, 5.45; alveolar length of maxillary toothrow, 3.15; width across maxillary toothrows, 4.20; bullar length, 8.00; width across bullae, 12.40; length of interparietal, 3.10; width of interparietals, 3.75; length of nasal, 7.90; width of nasals, 2.35; width of rostrum, 3.60; least interbullar distance, 4.00; length of mandibular toothrow, 2.80.

Distribution.—Sandy areas in arid grassland associations in and around the Great Sand Dunes of the San Luis Valley, Colorado (Fig. 23).

Diagnosis.—See Table 5, sample 13, for measurements. Size medium, with tail relatively longer than other populations. Skull with broadest interorbital region, short nasals, and shortest and narrowest interparietals; bullae relatively small, molariform, teeth relatively narrow, expecially premolars and M^1. Color dark and rich (Table 11, Fig. 15).

Comparisons.—See account of *P. f. apache* for remarks on distinguishing *P. flavus.* Skull smaller, interorbital region wider, and interparietals smaller than *P. f. caryi.* Size generally larger, interorbital region much wider, and interparietals shorter and narrower than *P. f. melanotis.*

Remarks.—Goldman (1938) assigned all of the relatively dark-colored specimens of Apache pocket mice from New Mexico, including those from Gran Quivira, Santa Fe, Pecos, Glorieta, and Burford Lake to *P. a. relictus.* The Gran Quivira specimens are referred to *P. f. melanotis,* and the Pecos, Santa Fe, Glorieta, and Burford Lake specimens are assigned to *P. f. caryi.*

Records of occurrence.—Specimens examined, 26, distributed as follows: COLORADO. *Alamosa Co.:* 1.4 mi N, 9.6 mi E Mosca, 2 (MSB); 1.4 mi N, 11 mi E Mosca, 1 + chromosomes (MSB); Medano Ranch, 15 mi NE Mosca, 1 (BS), 2 (MVZ), 7 (UCM); Great Sand Dunes National Monument, 1.6 mi NE Headquarters Medano Springs Ranch, 11 (MVZ); 3 mi S Great Sand Dunes National Monument, 1 (MVZ).

Additional records.—COLORADO. *Alamosa Co.:* Great Sand Dunes National Monument (Armstrong, 1972).

Perognathus flavescens melanotis Osgood, 1900

1900. *Perognathus apache melanotis* Osgood, N. Amer. Fauna, 18:27, 20 September.

1929. *Perognathus gypsi* Dice, Occas. Papers Mus. Zool., Univ. Michigan, 203:1, 19 June; holotype from White Sands, 12 mi SW Alamogordo, Otero Co., New Mexico.

1933. *Perognathus apache gypsi*, Benson, Univ. California Publ. Zool., 40:26, 13 June.

Holotype.—Adult female (age class 5), skin and skull, BS 97416, from Casas Grandes, Chihuahua; obtained on 21 May 1899 by E. A. Goldman. Both skin and skull in good condition.

Measurements of holotype.—Total length, 133; length of tail, 65; length of hind foot, 19.5; occipitonasal length, 22.20; interorbital breadth, 5.10; alveolar length of maxillary toothrow, 2.85; width across maxillary toothrows, 4.20; bullar length, 7.60; width across bullae, 11.75; length of interparietal, 2.60; width of interparietals, 3.95; length of nasal, 8.25; width of nasals, 2.25; width of rostrum, 3.65; least interbullar distance, 4.20; length of mandibular toothrow, 2.70.

Distribution.—Sandy areas in desert and grassland associations from Gran Quivira and the San Augustine Plains, New Mexico, southward to the Samalayucca Sands and Casas Grandes, Chihuahua; and extending west from El Paso Co., Texas to Willcox Playa, Arizona (Fig. 23).

Diagnosis.—See Table 5, samples 16, 17, 18, and 19 for measurements. Size small in most dimensions, with relatively short tail. Size varies altitudinally and latitudinally, being largest in the higher, northern populations and smallest in the Deming Plains and Jornada del Muerto populations. Skull short, but with relatively large bullae; interparietals not noticeably broadened. Color extremely variable geographically, from white with a grayish overwash (White Sands) to relatively dark and rich (Jornada del Muerto and Casas Grandes, Table 11 and Fig. 15).

Comparisons.—More similar in size and proportions to *P. flavus* than the more northern populations of *P. flavescens*. Interorbital breadth 4.9 mm or greater in *P. f. melanotis*, and 4.7 mm or less in *P. flavus;* posterior cranial region more constricted and bullae more inflated in *P. flavus,* least interbullar distance averages 2.90 mm in *P. flavus* and 3.95 mm in *P. f. melanotis*. See account of *P. f. apache* for additional remarks on distinguishing *P. flavus*. *P. f. melanotis* differs from *P. f. copei* in larger size; the skull of *P. f. melanotis* has a narrower interorbital region, the interparietals are shorter and narrower, the interbullar region is more constricted, and the articular process of the mandible is shorter than in *P. f. copei*.

Remarks.—The San Augustine Plains and Gran Quivira populations approach the Rio Grande Valley population of *P. f. caryi* in most characters. Members of the White Sands population have relatively large feet, inflated bullae, and wide rostra, and approach *P. f. copei* in having wide interorbital regions and long interparietals. The individuals from Willcox Playa were too few to adequately assess their morphologic features. However, other than a slight color difference (Table 12), that sample did not appear to be materially different from specimens from near Lordsburg and from Casas Grandes. Bailey (1932) allied all of the relatively dark-colored samples of Apache pocket mice from New Mexico, including those from Pecos, Santa Fe, Glorieta, Burford Lake, and Gran Quivira with the holotype of *P. a. melanotis* from Casas Grandes, but assigned specimens from Deming to *P. a. apache*. Goldman (1938) later assigned the dark-colored specimens from New Mexico to *P. a. relictus,* restricted *P. a. melanotis* to the holotype, and retained the Deming specimens under *P. a. apache*. These latter specimens (BS collection) were dug from a burrow, and are too young to show any characteristics useful for distinguishing subspecies.

Records of occurrence.—Specimens examined, 148, distributed as follows: Arizona. *Cochise Co.:* 3 mi SE Willcox, 4,163 ft, 5 (MVZ). New Mexico. *Catron Co.:* 15 mi S, 15 mi W Magdalena, 1 (DCBML). *Doña Ana Co.:* 6 mi W La Mesa, 1 (ENMU); 7 mi N, 2 mi E Las Cruces, 1 (UA); 6 mi E Las Cruces, 1 (NMSU); 13 mi SW Las Cruces, 1 (NMSU). *Hildago Co.:* 11 mi N, 10 mi W Lordsburg, 1 (ENMU). *Luna Co.:* Deming, 3 (BS). *Otero Co.:* White Sands, 10 mi SW Tularosa, 5 (MVZ); Quartz Sands, 14 mi SW Tularosa, 4,100 ft, 18 (MVZ); White Sands, 12 mi W Alamogordo, 8 (MVZ); White Sands, 18 mi W Alamogordo, 4 (AMNH), 5 (MVZ); 15 mi SW Alamogordo, 1 (LACM); White Sands, 18 mi SW Alamogordo, 32 (MVZ); White Sands, 1 (LACM), 2 (UMMZ); Walker Ranch, White Sands National Monument, 1 + chromosomes (MSB); Interior of White Sands, 3 (UMMZ). *Sierra Co.:* 1 mi N, 4.5 mi E Engle, 1 (MSB); 1 mi S, 5.4 mi E Engle, 3 + chromosomes (MSB). *Socorro Co.:* Mesa Jumanes, southern portions, 1 (BS); Mesa Jumanes, Ruins of Gran Quivira, 1 (BS); Gran Quivira National Monument, T1S, R8E, 13 (MSB); San Augustine Plains, 12 mi E, 10 mi S Datil, 1 (MSB); San Augustine Plains, sec. 28–29, T2S, R7W, 13 (MSB); San Augustine Plains, 12 mi NW Monica Spring, 4 (BS); Gallina Mountains, 2 (BS). Texas. *El Paso Co.:* 7.5 mi E City Hall, El Paso, 1 (KU); 19.4 mi E El Paso, 1 + chromosomes (MSB); 2.5 mi N Ysleta, 10 (UIMNH); 3 mi E Ysleta, 1 (MALB). Chihuahua. 1 mi E Samalayucca, 1 (MVZ); 2.5 mi S, 2 mi W Samalayucca, 1 (KU); 10 mi SE Zaragosa, 1 (KU); Rio Casas Grandes, 9 mi N Nueva Casas Grandes, 1 (MSB); 1 mi E Rio Casas Grandes, 10 mi N Nueva Casas Grandes, 4 + chromosomes (MSB).

Other Specimens Examined

Perognathus fasciatus fasciatus.—Specimens examined, 33, distributed as follows: Montana. *Roosevelt Co.:* 9 mi SE Baineville, 4 (UMMZ). North Dakota. *Billings Co.:* 1 mi S, 1 mi W Medora, 2,300 ft, 10 (KU). *Burleigh Co.:* 9 mi E Bismark, 5 (UMMZ). *Kidder Co.:* 6 mi W Steele, 6 (UMMZ). *Pembina Co.:* Weeks Farm, sec. 36, T160N, R56W, 1 (MSB). *Stutsman Co.:* 7 mi N Jamestown, 1 (UMMZ); 14 mi W Jamestown, 4 (UMMZ). South Dakota. *Todd Co.:* 15 mi W Mission, 1 (MSB). *Walworth Co.:* Molstad Lake Park, 1 (KU); Swan Creek, 13 mi S Selby, 1,600 ft, 1 (KU). Nebraska. *Cherry Co.:* Sparks, 1 (UMMZ); Ft. Niobrara Game Reserve, 1 (UNSM).

Perognathus fasciatus olivaceogriseus.—Specimens examined, 44, distributed as follows: Montana. *Carter Co.:* Ekalaka Hills, 4.5 mi S, 1 mi E Ekalaka, (MMNH). Nebraska. *Banner Co.:* 10 mi S, 2.5 mi E Gering, 3 (VMKSC). *Dawes Co.:* 1 mi SW Chadron, 1 (UNSM). *Sioux Co.:* 5.5 mi W Crawford, 6 (UNSM); 6 mi W Crawford, 1 (UNSM); Glenn, 1 (UNSM); 3 mi N Glenn, 2 (UNSM); 3.5 mi N, 1 mi E Glenn, 3 (UNSM); 8 mi W Ft. Robinson, 1 (UNSM). South Dakota. *Jackson Co.:* 7 mi SW Kadoka, 1 (MMNH). Wyoming. *Carbon Co.:* 1 mi E Ft. Steele, 13 (MSB), 2 + chromosomes (MSB). *Converse Co.:* Van Tassel Creek, 1 (CM). *Johnson Co.:* 2 mi S, 6.5 mi W Buffalo, 5,620 ft, 3 (KU). *Sheridan Co.:* 5 mi NE Clearmont, 3,900 ft, 1 (KU).

Perognathus fasciatus infraluteus.—Specimens examined, 7, distributed as follows: Colorado. *El Paso Co.:* Air Force Academy, 10 mi N Colorado Springs, 4 (CAS); 6 mi N, 1 mi W Colorado Springs, 2 (UIMNH). *Huerfano Co.:* 4 mi S LaVeta, 7,000 ft, 1 (KU).

Perognathus fasciatus litus.—Specimens examined, 31, distributed as follows: Wyoming. *Natrona Co.:* 5 mi W Independence Rock, 6,000 ft, 4 (KU). *Sweetwater Co.:* 25.4 mi N Table Rock, 25 (MSB), 2 + chromosomes (MSB).

Perognathus fasciatus callistus.—Specimens examined, 30, distributed as follows: Colorado. *Moffatt Co.:* N Bank Yampa River, 5 mi NW Cross Mountain, 1 (CM). *Rio Blanco Co.:* 16 mi W Meeker, 3 mi up Scenery Gulch (N of White River), 1 (CM). Utah. *Dagget Co.:* 0.5 mi SW Clay Basin Camp, 6,300 ft, 2 (UU); Bridgeport, 1 (UU). *Uintah Co.:* West Rim, Dead Man Bench, opposite Leota Flats (W of Green River), 2 (CM); E Green River, 3 mi S Jensen, 1 (CM); 4.6 mi N Bonanza, 1 (MSB), 3 + chromosomes (MSB); Bonanza, 1 (UU); 1 mi S, 1.5 mi E Bonanza, 1 + chromosomes (MSB); 13.4 mi E Ouray, 1 + chromosomes (MSB). Wyoming. *Sweetwater Co.:* Kinney Ranch, 6,900 ft, 21 mi S Bitter Creek, 6 (KU); Kinney Ranch, 21 mi S Bitter Creek, 7,100 ft, 2 (MVZ); Kinney Ranch, sec. 8, T15N, R98W, 23 mi SW Bitter Creek, 1 (MVZ); Shell Creek, 25 mi S Bitter Creek, 5 (CM); Blacks Fork, opposite mouth, 5,930 ft, 1 (UU).

Perognathus flavescens flavescens.—Specimens examined, 90, distributed as follows: Colorado. *Adams Co.:* Barr, 1 (UCM). *El Paso Co.:* Sandy Gulch, 2 mi E center Colorado Springs, 6,000 ft, 1 (UCM). *Washington Co.:* Akron, 5 (UMMZ); 8 mi W Akron, 1 (UMMZ). *Yuma Co.:* N of Wray, 2 (UCM). Nebraska. *Antelope Co.:* Clearwater, 1 (UMMZ); Neligh, 1 (MVZ), 1 (UNSM). *Banner Co.:* 10 mi S, 2.5 mi E Gering, 4 (VMKSC). *Cherry Co.:* Hackberry Lake, Valentine National Wildlife Refuge, 2 (KU), 18 (UMMZ); 4 mi E Valentine, 1 (KU); 2 mi E Valentine, 1 (KU); Kennedy, 5 (MVZ), 1 (UMMZ); 4 mi S Kennedy, 1 (UNSM); 2 mi E Kennedy, 3 (KU); 4 mi E Kennedy, 2 (KU); 18 mi NW Kennedy, 1 (UNSM); Niobrara River, 10 mi S Cody, 1 (UNSM); 11.5 mi S, 0.5 mi W Nenzel, 3,000 ft, 1 (VMKSC). *Custer Co.:* 1 mi S, 2 mi W Broken Bow, 2 (VMKSC). *Garden Co.:* Crescent Lake National Wildlife Refuge Headquarters, sec, 29, T21N, R44W, 3 (VMKSC); 0.75 mi E Crescent Lake National Wildlife Refuge Headquarters, sec. 29, T21N, R44W, 1 (VMKSC); 3 mi SE Crescent Lake National Wildlife Refuge Headquarters, 4 (VMKSC); 5 mi S Crescent Lake National Wildlife Refuge Headquarters, 1 (VMKSC). *Hooker Co.:* Kelso, 7 (UMMZ). *Kearney Co.:* 10 mi N, 1 mi E Axtell, 6 (VMKSC); 5 mi S, 2 mi E Kearney, 6 (VMKSC); Doby Town, 5 mi S, 3 mi E Kearney, 1 (VMKSC). *Keith Co.:* N side Kingsley Reservoir, 1 (UNSM). *Lincoln Co.:* 1 mi N Brady, 1 (UNSM); 2.5 mi N, 4.5 mi E North Platte, 1 (VMKSC). *Sheridan Co.:* 14 mi W Lakeside, 1 (MVZ). *Thomas Co.:* Halsey National Forest, 1 (VMKSC).

Perognathus flavescens perniger.—Specimens examined, 22, distributed as follows: Iowa. *Freemont Co.:* Randolph, 1 (UNSM). Minnesota. *Sherburne Co.:* Elk River, 1 (UCM), 5 (MVZ); Sand Dune State Park, 3 (MMNH); 6 mi E St. Cloud, 5 (UMMZ). South Dakota. *Bon Homme Co.:* 0.3 mi N, 0.3 mi E Springfield, 2 (MSB). *Clay Co.:* 1.5 mi N Vermillion, 3 (MSB); 1 mi W Vermillion, 1 (MSB); 3.5 mi N, 0.5 mi E Meckling, 1 (MSB).

Perognathus flavescens cockrumi.—Specimens examined, 5, distributed as follows: Kansas. *Barber Co.:* 2 mi N, 2 mi W Sharon, 2 (SIUC). *Geary Co.:* Junction City, 1 (UCM). *Harvey Co.:* Section N of Harvey Co. Park, 2 (KSU).

Perognathus flavescens copei.—Specimens examined, 54, distributed as follows: New Mexico. *Chaves Co.:* 3 mi N, 9 mi W Caprock, 4 (MSB), 3 + chromosomes (MSB); 7 mi E Hagerman, 1 (MSB). *Eddy Co.:* 1 mi N, 26.5 mi E Carlsbad, 2 (ENMU). *Lea Co.:* 29 mi E Carlsbad, 1 (ENMU); 3 mi S, 29 mi E Carlsbad, 2 (ENMU); 2.5 mi S, 31 mi E Carlsbad, 1 (ENMU); 7 mi N, 15 mi W Jal, 2 (MSB). *Quay Co.:* 2 mi S, 0.5 mi E Logan, 1 (MSB). *Roosevelt Co.:* 3.3 mi S Tolar, 3 + chromosomes (MSB); 3.25 mi N, 1 mi E Portales, 1 (ENMU); 9 mi S Portales, 1 (ENMU); 4.5 mi S, 3 mi W Portales, 1 (ENMU). *Union Co.:* Perico Creek, 4 mi S Clayton, 3 (MSB). Oklahoma. *Woods Co.:* Waynoka, 10 (UMMZ). Texas. *Andrews Co.:* 14 mi S Andrews, 3 (UMMZ). *Haskell Co.:* 7 mi SW Rochester, 1 (MWU). *Hemphill Co.:* Gene Howe Refuge, 5 mi NE Canadian, 1 (TCWC). *Loving Co.:* 11 mi E Mentone, 1 + chromosomes (MSB). *Roberts Co.:* 6 mi N Miami, 4 (MWU); 7 mi N Miami, 1 (MWU). *Scurry Co.:* 4 mi SW Snyder, 4 (MWU). *Ward Co.:* 4 mi NE Monahans, 1 (UIMNH). *Wheeler Co.:* 1 mi W Mobeetie, 2 (MVZ).

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